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H. C. GILSON

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PLANKTON AND WATER MOVEMENTS IN WINDERMERE

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(With 15 Figures in the Text)

INTRODUCTION

Ragotzkie & Bryson (1953) derived an equation describing the effects of water movements on the distribution of *Daphnia pulex* in a bay of Lake Mendota. This equation rests on the assumptions that the animals do not carry out any purposeful horizontal movements and that they control their vertical orientation by means of some factor independent of the movements of the water, such as the vertical light gradient from the surface. This implies that the animals will tend to maintain a constant depth in spite of vertical currents. The equation is:

$da/dt = \text{Diffusion} - [a.dv_x/dx - v_x.da/dx]$

where a = concentration of *Daphnia*, x = the direction of the horizontal current, and v_x = the velocity of the current.

The middle term on the right hand side describes the horizontal transport and the last term describes the horizontal velocity divergence or convergence. Diffusion may be ignored. Horizontal transport implies that existing variations in the distribution will be transported past a given point in the direction x and with a velocity v_x. The horizontal velocity divergence or convergence will produce variations in the distribution. Along a line where the horizontal velocity is increasing and the vertical velocity decreasing there will be dispersion, while along a line where the horizontal velocity is decreasing and the vertical velocity is increasing there will be concentration.

The object of this investigation was to find out whether the factors given in the above equation are important in determining the horizontal distribution of the planktonic crustacea of Windermere. The water movements in Windermere have been described by Mortimer (1951, 1952). The most important features are the response to wind stress and the resulting uninodal internal seiches. Fig. 1 shows the pattern of water velocities during a uninodal internal seiche in a rectangular lake basin. The figure shows the simplest case, when the thermocline is horizontal. The lengths of the arrows indicate the relative magnitudes of the velocity of the current. The arrows in the hypolimnion show the actual direction of the current and the arrows in the epilimnion show the horizontal and vertical components of velocity. The velocities vary with distance from the node, the vertical velocities increase from zero at the node to a maximum at the ends of the basin. The horizontal velocities decrease from a maximum at the node to zero at the ends of the basin.

The expected effects of water movements on the horizontal distribution of zooplankton were worked out as the result of the study of several sets of collections of the zooplankton in Windermere and from the application of Ragotzkie & Bryson's equation to the water movement situation described by Mortimer (1951, 1952). Although this is one of the results of this investigation it is convenient to describe it at this stage as it will simplify the explanation of the planning and results of the sampling.

The expected effects of a uninodal internal seiche are shown in Figs. 2 *a-d*. The selected initial condition (*a*) is similar to that given in Fig. 1; the distribution of animals in the epilimnion, shown by dots, is assumed to be uniform. Fig. 1 shows that to the right of the node, where the thermocline is sinking, horizontal convergence occurs and the concentration of animals should increase. To the left of the node horizontal divergence occurs and the concentration of animals should decrease. In Fig. 2*b* the thermocline has tilted to its maximum extent and the

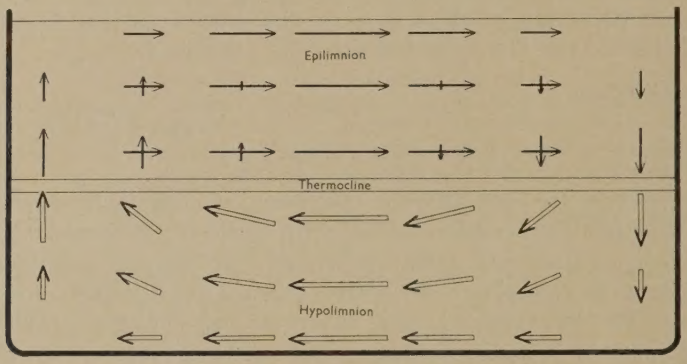

Fig. 1. A longitudinal section of a stratified lake showing the distribution of water velocities during a uninodal internal seiche. The lengths of the arrows indicate the relative magnitudes of the velocity of the current. The arrows in the hypolimnion show the direction of the current, and the arrows in the epilimnion show the vertical and horizontal components of velocity.

position of the dots in the epilimnion shows the expected distribution of the animals. Fig. 2*c* shows the expected distribution when the thermocline has tilted the other way. The water movements involved in a seiche are reversible, which means that any concentration and dispersion produced when the thermocline is tilted are reversed when the thermocline returns to the horizontal. Thus whenever the thermocline is horizontal, between each swing and in the final state when the oscillation has ceased (Fig. 2*d*), the distribution of the plankton should be the same as in the initial condition.

Figs. 2 *e-h* show the expected effect of wind. The wind exerts a stress on the surface of the lake which is balanced by a very small tilt of the surface itself, which may be ignored, and by a much larger tilt of the thermocline. The water movements associated with this tilt should increase the concentration of animals in the epilimnion at the leeward end of the lake (Fig. 2*f*). If the wind blows hard enough

and long enough the water in the epilimnion circulates. This should increase the concentration of animals at the leeward end of the lake still further and produce an area at the windward end almost devoid of animals (Fig. 2*g*). If the change in concentration produced by the wind is greater than that produced by an equal thermocline tilt during a seiche then the seiche resulting from the removal of the wind stress should not entirely smooth out the changes in concentration produced by the wind stress. All the smoothing should occur when the thermocline swings back to the horizontal from the position in Fig. 2*g*. The distribution produced in this way should not be permanently effected by the subsequent swings of the

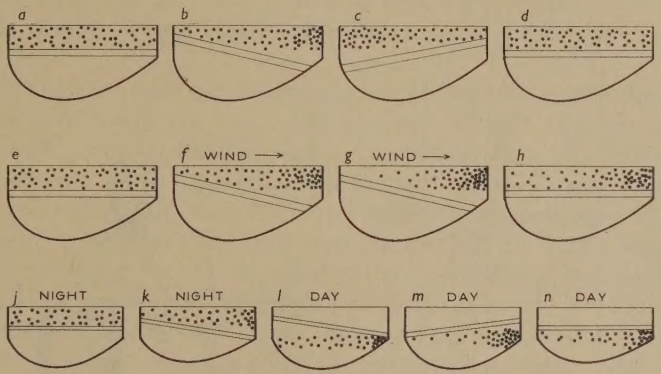

Fig. 2. Longitudinal sections of a stratified lake showing the expected effects of water movements on the horizontal distribution of zooplankton. The distributions of the animals are indicated by dots.
a-d, the expected effects of a uninodal internal seiche;
e-h, the expected effects of wind stress;
j-n, the expected effects of a uninodal internal seiche combined with diurnal vertical migration through the thermocline.

thermocline. In this way, wind should cause permanent changes in the distribution of animals in the epilimnion.

In Figs. 2 *j-n* is shown one possible result of the combined effects of a uninodal internal seiche and diurnal vertical migration through the thermocline. Figs. 2*j* and *k* are similar to *a* and *b*. It is assumed that the animals migrate down through the thermocline while it is still at its maximum tilt. The swing of the thermocline should then produce further concentration at the right hand end of the basin (Figs. 2*l* and *m*). It is assumed that the seiche ends before any further migration takes place. The expected final pattern of distribution is shown in Fig. 2*n*. Here again a permanent change in the distribution should be produced.

These diagrams show in an idealized form the expected effects of water movements on the distribution of zooplankton. The actual distributions will depend on such factors as the strength and direction of the wind, the amplitude of the resulting seiches, the relative timing of the seiches and diurnal vertical migration, and the degree of correction for vertical displacement shown by the animals.

METHODS

(*a*) *Sampling methods*

A pump and hose sampler was used for making horizontal collections. The pump was a 'Jabsco' self-priming pump driven by an electric motor at a speed of about 1100 r.p.m., power being provided by a small petrol generator. The suction hose was 2 cm internal diameter reinforced rubber pipe. Usually about 10 m of pipe were used which gave a delivery rate of about 40 litres/min.

Fig. 3*a* is a diagram of the whole apparatus. The water passed from the intake

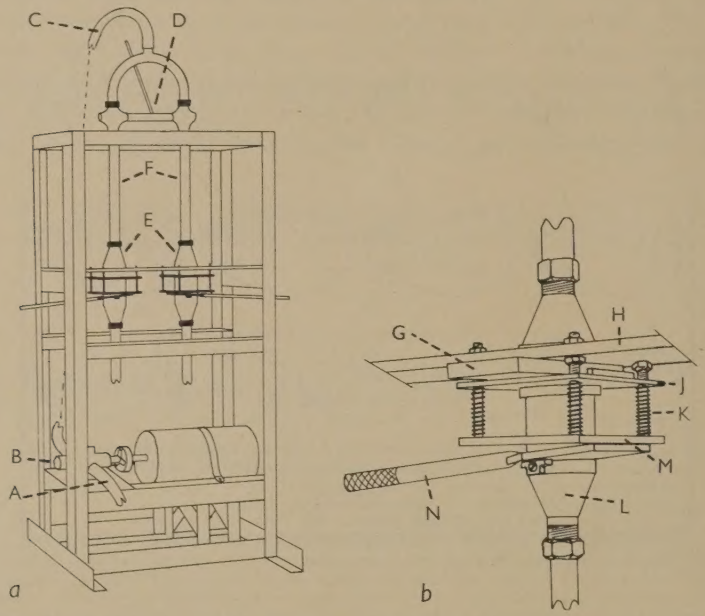

Fig. 3. The pump and hose sampling apparatus: *a*, the complete apparatus; *b*, one of the filter chambers.

A, intake hose
B, pump
C, connecting pipe
D, two-way tap
E, filter chamber
F, soft rubber tube
G, filter carrier
H, supporting plate
J, floating plate
K, springs
L, conical flange
M, lower fixed plate
N, lever for releasing filter carrier

pipe (*A*) through the pump (*B*) and up a pipe (*C*) at the back of the apparatus to a two-way tap (*D*) and then to one of the two filter chambers (*E*). Fig. 3*b* is a diagram of one of the filter chambers. The filter was a piece of 60-mesh bolting silk, cut 8 cm square laid over a 5 cm diameter hole in a rectangular block of ebonite (*G*). This was held in the chamber between a rubber washer stuck to the top plate (*H*) and a floating plate (*J*) which was held up firmly by springs (*K*). The conical flange (*L*) was fastened to the floating plate but passed through a hole in the lower fixed plate (*M*). The ebonite block carrying the filter could be

removed by depressing the lever (*N*) thus lowering the floating plate. No support for the bolting silk was necessary, the pressure of the springs forcing it against the rubber washer being sufficient to hold it in place.

At the start of a collecting run, a filter was put into place in each chamber and after pumping through one chamber for one minute the tap was changed over. To remove the water remaining above the filter now turned off, the rubber tubing connecting the filter chamber to the tap (Fig. 3, *F*) was squeezed several times. The lever was depressed and the ebonite block carrying the filter was carefully removed and another put in its place. At the end of the second minute the same procedure was carried out on the other filter chamber. This procedure was repeated at 1 minute intervals for the whole of the run. Between each change-over the filter carrying the sample just collected was removed from its carrier and a clean filter put in its place.

This apparatus was used for making continuous horizontal collections from a launch. The launch was run at a speed of about 5 knots on a zig-zag course between known points on the lake shore. The end of the intake hose was held at a depth of about 4·5 m. Changing the filters at 1 minute intervals meant that one sample was collected for each 150 m travelled by the launch. The exact speed of the launch varied with the weather conditions, but the number of samples collected on each leg of the run was noted so that the length of each sample could be calculated. It was difficult to hold the end of the hose pipe at a known depth with the launch travelling at 5 knots. After several unsuccessful attempts the hose pipe was pushed down inside a 20 ft length of $2\frac{1}{2}$ in. steel pipe. The upper end of the pipe was lashed loosely to a bollard on the quarter of the launch and a pair of guy ropes was carried forward from the bottom of the pipe to a point just forward of the beam, with the pipe inclined forward at an angle of about 40° to the vertical. This arrangement worked very well; there was some vibration occasionally but even in rough water the pipe remained remarkably stable.

Divided vertical hauls were also made with a Clarke-Bumpus sampler modified as a vertical closing net.

(*b*) *Temperature measurements*

Thermistor thermometers were used for all temperature measurements. The continuous temperature records shown in Figs. 7 and 8 were constructed by drawing isotherms on continuous plots of temperature from nine depths (1, 5, 8, 11, 15, 20, 25, 32 and 40 m) taken at the Slape Scar buoy (Fig. 4). The use of thermistors and the continuous recording apparatus are described in Mortimer & Moore (1953). Fig. 4*b* is a diagram of the temperature profile of the lake based on measurements made at the Watbarrow buoy at intervals of about 10 days during the period March 1955 to July 1956.

(*c*) *Counting methods*

The animals in a sample were filtered through a small disc of perforated cellophane. The animals on the cellophane were gathered together in a bunch and

counted under a low power binocular microscope by separating them one by one from the bunch; each was identified and recorded. Because many of the samples contained too many animals to be counted entirely, a volumetric method of subsampling was used to reduce the size of the samples

RESULTS

The theory described in the introduction was developed as the result of the study of a number of collections made between May 1955 and June 1956. The

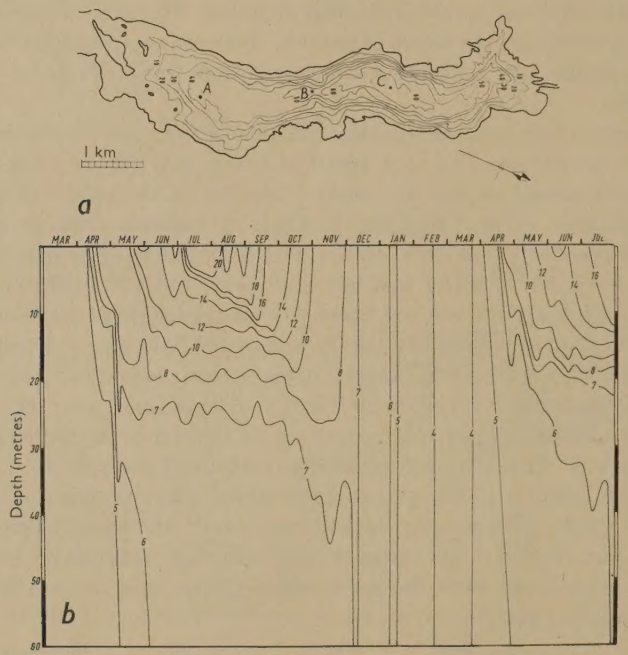

Fig. 4. *a*, Bathymetrical map of the north basin of Windermere showing the positions of the three buoys that were used as sampling stations: *A*, Slape Scar; *B*, Red Nab; *C*, Watbarrow. *b*, Temperature profile (° C) for the Watbarrow buoy for the period March 1955 to July 1956.

first series of collections, made in May 1955, was designed to find out whether there was or was not a pattern in the horizontal distribution of the plankton.

(*a*) *The collections of May 1955*

The collections were made with the continuous horizontal sampler. The end of the intake hose was held at a depth of 4·5 m. A selection of the plankton distributions are shown in Figs. 5 and 6; wind and temperature data are illustrated in Fig. 7.

It is possible to explain the plankton distributions shown in Figs. 5 and 6 in terms of wind and water movements. The strong SW winds of 4 and 5 May pro-

bably produced an accumulation of surface water at the north end of the basin; the diagram for the collection of 5 May (Fig. 5) shows larger numbers of animals at the north end of the basin. The NNE wind of 13 May probably produced an accumulation of surface water at the south end of the basin; this is also indicated by the isotherms. The diagram for the collection of 13 May (Fig. 5) shows larger numbers of animals at the south end of the basin. The pattern producing water movements described in the introduction can only occur when a thermocline is

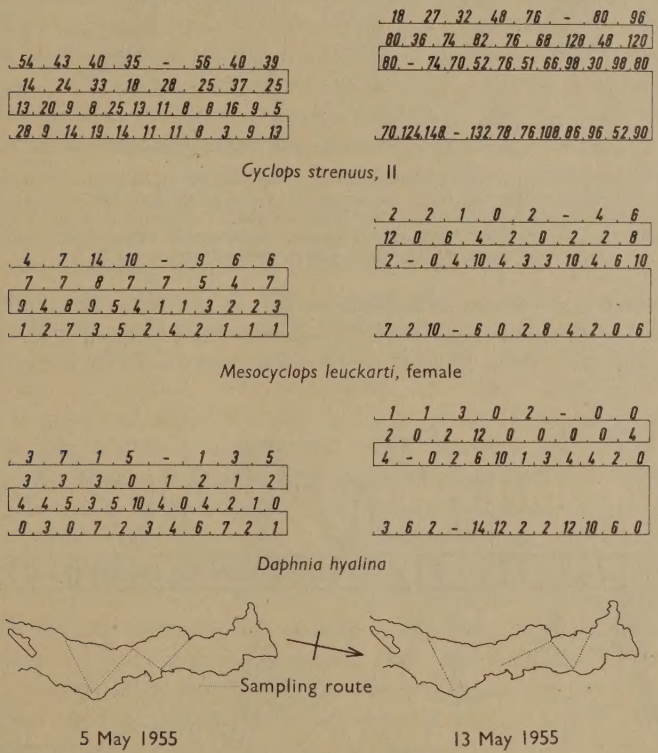

Fig. 5. The numbers of three species in the samples of the horizontal collections of 5 and 13 May 1955. The numbers are shown in their positions along the sampling route, which is shown as a pecked line in the accompanying maps, with north at the tops of the diagrams.

present. Since the isotherm diagram (Fig. 7) shows that a thermocline was not established until 11 May, it is not surprising that no clear pattern of distribution was found on 5 or 13 May. Oscillations of the thermocline occurred between 13 and 15 May and again between 18 and 20 May, following the ENE wind of 17 May. Fig. 6 shows that there was a clear distribution pattern on 20 May. The results of these collections demonstrated that there was a possible connection between water movements and the horizontal distribution of zooplankton.

(b) The collections of October 1955

The next series of collections was designed to study the effects of water movements on the numbers of animals at a fixed point. A series of divided vertical hauls

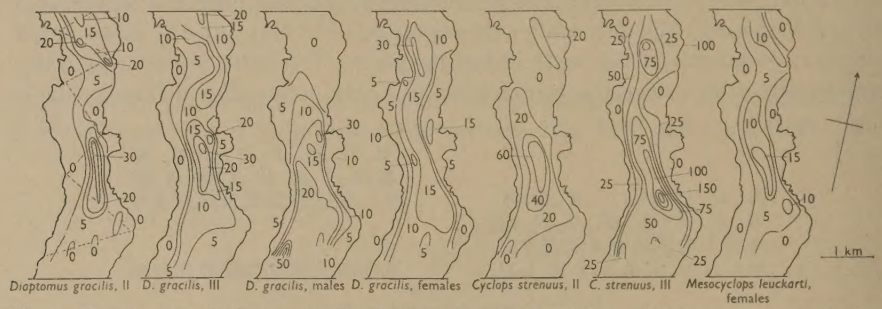

Fig. 6. Maps showing the horizontal distributions, at a depth of 4·5 m, of the more common species and stages as indicated by the horizontal collection of 1310 h on 20 May 1955. The counts of the various species and stages were plotted on their positions along the sampling route, which is shown in the left-hand map, and contours were drawn by eye. For the sake of clarity the original counts have been omitted. The figures show concentrations per 20 l.

was made, with a modified Clarke-Bumpus net, at the Slape Scar buoy (Fig. 4) four times a day for a period of 7 days, 28 September to 5 October 1955. The hauls were made from 35 to 25 m, 25 to 15 m, 15 to 5 m, and 5 m to the surface. At this

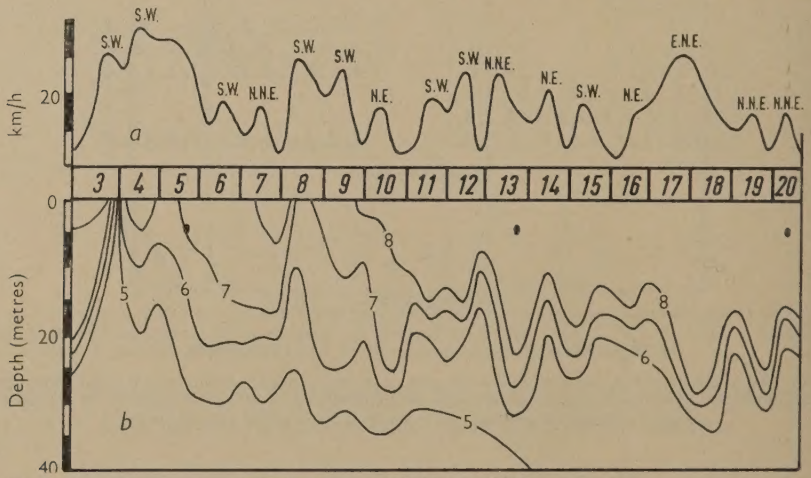

Fig. 7. Wind and temperature data for the period 3-20 May 1955: *a*, hourly means of wind speed and direction recorded by the Dines anemograph at The Ferry House; *b*, continuous isotherm plots (° C) from the temperature recorder at Slape Scar buoy. The times of the three horizontal collections made during the period are shown by dots.

time the thermocline lay between 10 and 20 m; thus, the first two hauls were below the mean depth of the thermocline and the last two above. Clear diurnal vertical migrations were shown by all the copepod species.

Seiche movements were expected to produce changes in the numbers of animals

at a particular station. When the thermocline sinks in the area of the station the animals in the epilimnion should be swept into or concentrated in the area. The animals in the hypolimnion should be swept out of or dispersed from the area of the station. The reverse should occur when the thermocline rises. Thus the expected changes were: (1) Thermocline sinking, increase in numbers above and decrease in numbers below the thermocline; (2) Thermocline rising, decrease in numbers above and increase in numbers below the thermocline. Vertical migration was a complicating factor because most of the copepods migrated through the thermocline; they were above it during the night and below it during the day.

Since a diagram giving the full results for all the species and stages would be rather large and complicated, several examples have been selected to include those which showed the clearest vertical migration, and *Daphnia* which showed practically no vertical migration. In Fig. 8 the results for a little more than 3 of the 7 days are shown as depth-time isopleth diagrams. The isopleths show the numbers per metre of haul; that is 1/10 of the counts for the 10-metre hauls and 1/5 of the count for the 5-metre haul. A depth-time isotherm diagram (see p. 221) for the corresponding period is reproduced in Fig. 8. Only the diagrams for *Diaptomus gracilis* stage V will be explained in detail. Between midnight of 29 September and noon of 30 September the thermocline rose slightly and then sank about 3 m, during which time *D. gracilis* V migrated down through the thermocline and its numbers decreased (thermocline sinking, decrease in numbers below the thermocline). Before haul E the thermocline started to rise and the haul contained larger numbers, still at the day depth below the thermocline (thermocline rising, increase in numbers below the thermocline). Between hauls E and F the thermocline continued at first to rise and then began to fall. *D. gracilis* V migrated up through the thermocline, and haul F contained very large numbers. The timing of the vertical migration probably coincided more or less with the peak of the thermocline displacement. Before the upwards migration the situation was a rising thermocline with increasing numbers below it; after the migration there was a sinking thermocline with increasing numbers above it. Thus the necessary conditions for increasing numbers probably occurred for most of the period between hauls E and F. Before haul G the thermocline continued to sink and then rose again. The animals migrated down through the thermocline and the numbers decreased. The relationship between thermocline movement and numbers was not so clear as three situations were involved: (1) thermocline sinking, increase in numbers above it; (2) thermocline rising, decrease in numbers above it; and (3) thermocline rising, increase in numbers below it. The observed decrease in numbers can be explained only if situation (2) had the greatest effect. Between midday and midnight of 1 October the sequence of events was similar to that of the same period of 30 September with the difference that the thermocline had only just started to fall by the time of haul J and that the increase in numbers was smaller.

Between midday of 3 October and midday of 4 October the connection between thermocline movements and numbers of animals was fairly clear. Initially the

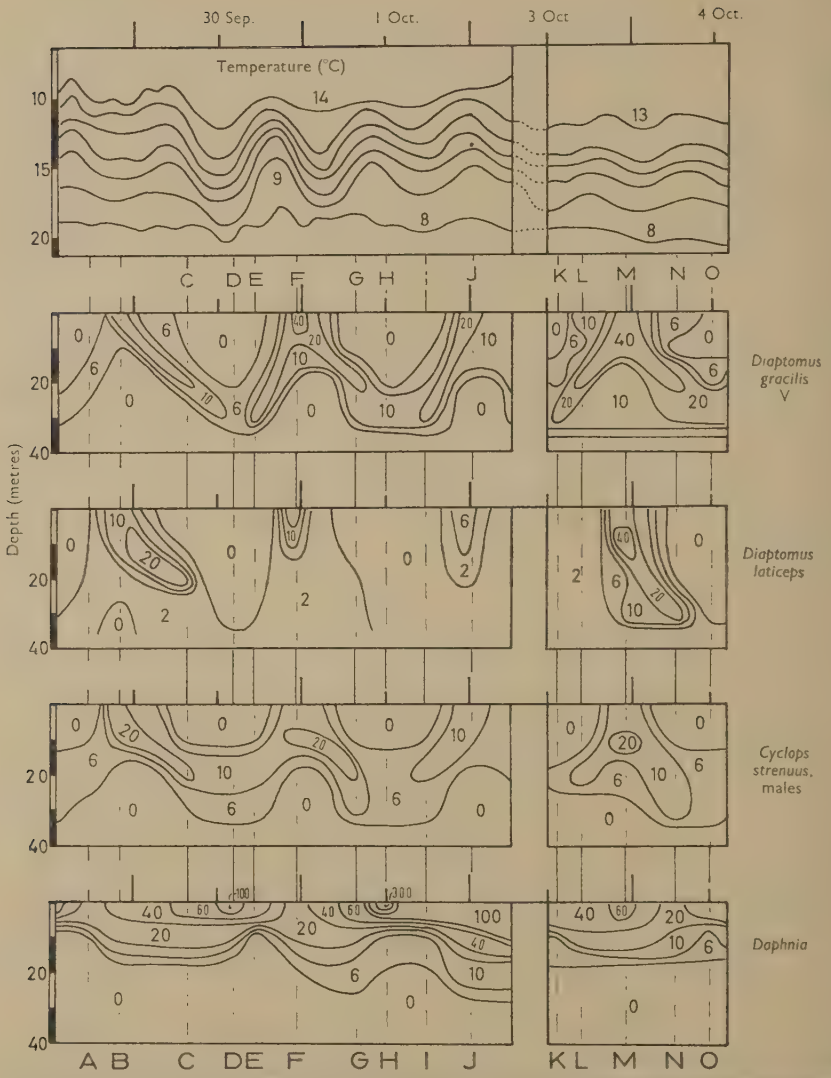

Fig. 8. Depth-time isotherm diagram (from the continuous temperature record) and isopleth diagrams for the series of divided vertical hauls taken at the Slape Scar buoy for 29 September to 4 October 1955. The contours were drawn by eye round plots of the counts of each species and stage placed at the mean depth of each division of the vertical hauls. The times of the vertical hauls are indicated by the thin broken lines and dates are given over the noon points. Successive hauls are labelled A, B, etc. The figures indicate the numbers per metre of haul.

thermocline was rising, the animals were at their day depth and numbers increased (thermocline rising, increase in numbers below the thermocline). Before haul M the thermocline started to fall, the animals migrated up through the thermocline and the numbers increased (thermocline sinking, increase in numbers above the thermocline). Between hauls M and N the sequence of events was similar to that of the same period of 30 October except that in this case the diagram shows that situation 2 (thermocline rising, decrease in numbers above the thermocline) was probably the dominant one. By the time of haul O the thermocline was falling and the numbers had decreased (thermocline sinking, decrease in numbers below the thermocline).

The pattern for the males of *Cyclops strenuus* was very similar to that of *Diaptomus gracilis* V. This was to be expected if they were both determined by similar vertical migrations and water movements. The stages of *D. laticeps* showed very similar patterns. The results for all the stages were combined and they have been shown in a single diagram in Fig. 8. This species carries out very extensive vertical migration and its day depth was actually greater than 40 m. It was generally absent from the day samples because the water at the Slape Scar buoy is 40 m deep. It was only present in appreciable numbers at night on a falling thermocline. It so happens this is true for all the nights shown in Fig. 8, but for the night of 1 October the thermocline had only just started to fall when haul J was made, and only small numbers of *D. laticeps* were present. On the night of 2 October (not shown in Fig. 8) the thermocline was rising at the time of the night haul and only very small numbers were found. Of the other species *Daphnia* showed the poorest correlation with the movements of the thermocline. The major deviations from the expected behaviour were shown by hauls F and G.

Two further series of collections were planned, combining vertical and horizontal collections. These series were carried out in March and June 1956. In the March series the lake was isothermal and no attempt was made to measure temperature. The changes in distribution which occurred took place across the lake, in an east-west direction and they were not detected by the vertical hauls. In the June series, in addition to nightly horizontal collections, divided vertical hauls and vertical temperature profiles were taken at the Slape Scar, Red Nab and Watbarrow buoys (Fig. 4) four times a day for a period of 5 days. They yielded very little information because the amount of water movement which occurred during the series was very slight. In both series, however, the horizontal collections did yield useful information.

(*c*) *The collections of March 1956*

Table 1 shows the vertical distributions of adult male and female *Diaptomus gracilis* as the mean percentage of all the vertical hauls of the series. There was no perceptible vertical migration and the table shows that there was no clear vertical zonation either. The horizontal distributions of all the species and stages in the collections were very similar and only two examples, adult male and female *D. gracilis*, are shown in the distribution maps (Fig. 9). On 19 March the animals

occurred in greater numbers on the east side of the lake. Between the collections of 19 and 20 March the wind blew from between the NE and E, and in the collection of 20 March the animals were found in greater numbers on the western side of the lake. Between the collections of 20 and 21 March the wind blew from between the SE and E, and in the collection of 21 March the pattern indicated a movement away from the western side and a slight movement northwards. There

Table 1. *The mean percentage vertical distributions of male and female* Diaptomus gracilis *during the March 1956 series of collections*

Depth (m)	*D. gracilis* (%)	*D. gracilis* (%)
38–30	28	23
30–20	28	26
20–10	24	26
10–0	21	25

is a clear connection between the direction of the wind and the changes in the distribution of the animals. The absence of any vertical migration and vertical zonation probably means that the animals were not correcting their depth distribution with respect to vertical currents but were being carried passively in all directions by the movements of the water.

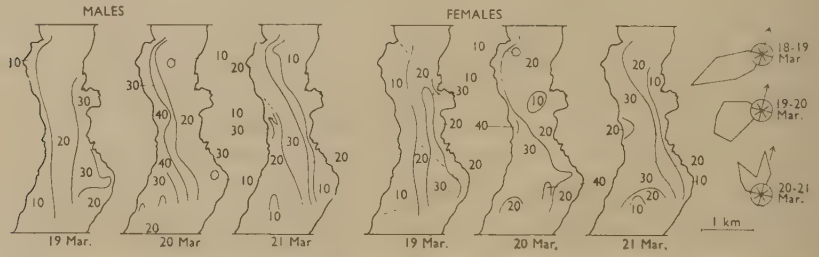

Fig. 9. The horizontal distributions of male and female *Diaptomus gracilis* at a depth of 4·5 m indicated by the horizontal collections made at 2000 h on 19, 20 and 21 March 1956. The figures show concentrations as numbers per 36 l. (see legend to Fig. 6). The wind roses were plotted by summing hourly means of wind speed for the 24 h before the collections were made in eighteen direction categories each of 20°. The distance of any point on the polygons from the circumference of the circle shows how much wind blew in that direction.

(*d*) *The collections of June 1956*

Fig. 10 shows histograms of the day and night vertical distributions of all the species and stages based on the means of all the hauls taken at 1050 h and 0015 h during the 5 days at the Watbarrow buoy. The histograms show that the majority of each species and stage was in the top 10 m at night. The sampling depth of the horizontal sampler was 4·5 m, and all the horizontal collections were made at night. Therefore the collections probably give a good picture of the horizontal distributions. To assist in the timing of this series, an overnight series of divided vertical hauls was made at the Watbarrow buoy about a week before. This

showed that there was no 'midnight sinking', probably because of the very short night at this time of year. It also indicated the amount of time available to take the night collections, as it was necessary for the animals to be at their night depths for the whole of the period.

Horizontal temperature profiles were taken simultaneously with the horizontal collections by means of a thermistor thermometer fastened to the end of the intake hose and read at 1 min. intervals. The depth of the profiles was the same as the sampling depth (4·5 m) which was above the thermocline. For most of the period of the series the sky was cloudy and practically no warming of the surface water occurred. There was a slight temperature gradient above the thermocline and therefore the higher temperatures on the isotherm maps indicate that the upper boundary of the thermocline was low, and vice versa.

The distribution maps for the second, third and fourth days of the series are shown in Fig. 11. The most convenient way to describe the connection between the

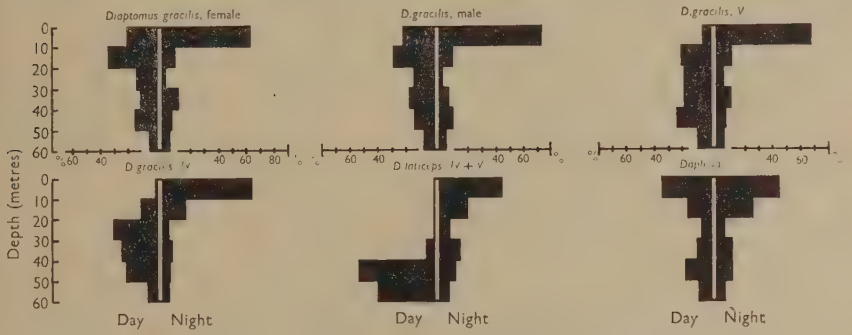

Fig. 10. Percentage vertical distributions by day and night at the Watbarrow buoy during the series of collections taken during June 1956.

distribution of the plankton and water movements is to consider the distribution of *Daphnia* which lay above the thermocline by day and night, and of *Diaptomus gracilis* IV which lay above the thermocline by night and below it by day. In June the nights are very short and this stage spent 18 or 19 h out of every 24 below the thermocline. Its distribution was therefore largely determined by events below the thermocline. The vertical series of September 1955 showed that there was an inverse relationship in time between the numbers of animals above and below the thermocline. This will happen if there is an inverse relationship in space between the horizontal distributions of animals above and below the thermocline. *Daphnia* should occur in greater numbers where the thermocline is low and *Diaptomus gracilis* IV should occur in greater numbers where the thermocline is high. The maps show that on all days an inverse relationship existed between the horizontal distributions of these two species. In addition there was also a clear connection between the distribution of *Daphnia* and the horizontal temperature profiles; higher numbers of *Daphnia* occurred where higher temperatures indicated a low thermocline.

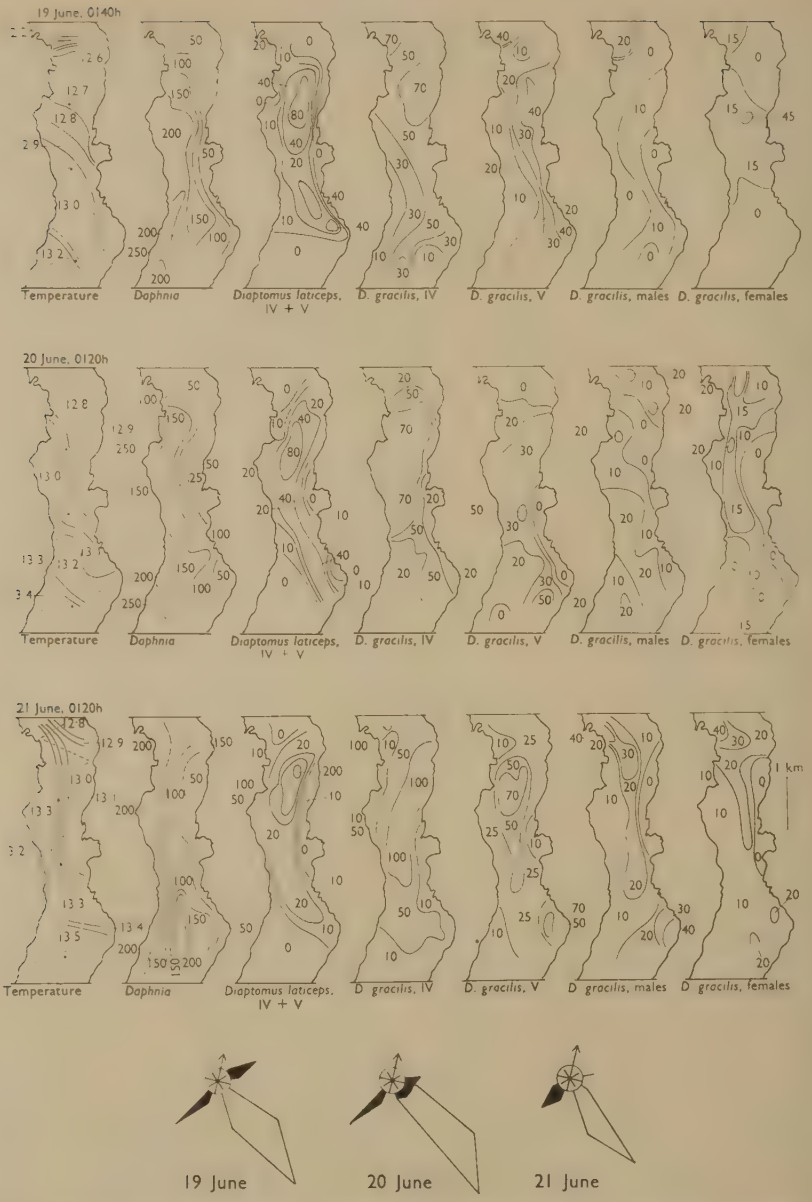

Fig. 11. The horizontal distributions of temperature and zooplankton, at a depth of 4·5 m, indicated by the horizontal collections made on 19-21 June 1956. The figures show numbers of animals per 10 l. (see legend to Fig. 6). As the prevailing wind during this period was about NE, a direction from which the anemometer at The Ferry House is sheltered, these records (shown as black polygons) are unreliable. The open polygons from wind data for Sellafield, a coastal station 37 km W of the lake, give a better picture of the wind over the lake as a whole.

On all the days the distribution of *Diaptomus gracilis* V was very similar to that of *D. gracilis* IV; this was to be expected because their day depths were very similar. The distribution of *D. laticeps* was similar also except that, as its distribution was limited by its day depth of over 40 m, the extent of its horizontal distribution was less. The distributions of *D. gracilis* male and female did not show any great similarity to either *Daphnia* or *Diaptomus gracilis* IV, and they were rather complicated on some of the days. Fig. 10 shows that by day the greatest numbers of *D. gracilis* male and female occurred between 10 and 20 m, that is in the zone of the thermocline. In this region the direction and velocity of the horizontal currents change rapidly with depth. This may be the reason for their rather complicated distributions.

THE STATISTICAL PROPERTIES OF THE DISTRIBUTIONS

There is a linear relationship between the mean and the standard deviation of the various species and stages present in each set of samples (Fig. 12); the slope of the line is usually about 0·5 and it cuts the standard deviation axis at a value of about 1. Fig. 13 shows the results of fitting Negative Binomial distributions to a selection of the results. The fit of the expected to the observed frequency distributions is quite good in each case.

The explanation usually offered when non-random distributions of plankton are found is that the animals are grouped into bunches or swarms. The maps in Figs. 6, 9 and 11 show that in the north basin of Windermere there were seldom more than one or two areas of high numbers; the distributions can hardly be described as swarm distributions. It has already been shown that it is quite probable that the horizontal distribution of the plankton is determined by water movements. It remains to be seen whether the statistical properties of the distributions can be explained in the same way.

It is possible to calculate the expected distribution of a species for a given thermocline tilt from the equation given by Ragotzkie & Bryson (1953), ignoring diffusion; and from the equation describing an internal seiche in a two-layered lake (Proudman 1953). The equations are

$$da/dt = -a.dv_x/dx - v_x.da/dx \qquad (1)$$

and,

$$v_x = C \sin x. \sin 2\pi t T^{-1}; \qquad (2)$$

where,

a = concentration of animals,
t = time,
v_x = velocity of horizontal current,
$x = L^{-1}\pi X$
X = any position along the mid-lake line,
L = the length of the basin,
C = a constant speed,
T = the period of oscillation.

What is required is an equation for a in terms of x and v_x. In equation (1) the term $v_x.da/dx$ describes the change in concentration at a given point produced by the horizontal transport of existing variations in the distribution. If it is supposed that initially, when the thermocline is horizontal, the horizontal distribution is

uniform, then $da/dx = 0$. This means that the changes in concentration produced when the thermocline tilts will be described by the term $a.dv_x/dx$, where dv_x/dx describes the horizontal convergence. Equation (5) is the equation of the concentration gradient produced in this way. But, as soon as the thermocline starts to

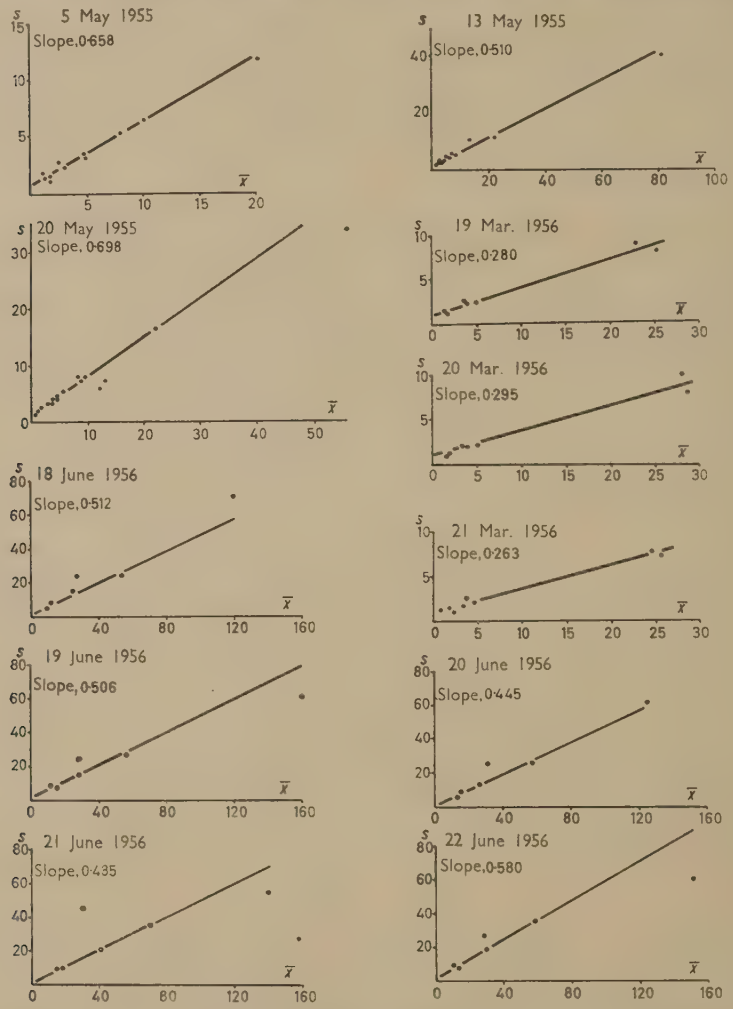

Fig. 12. Graphs of the mean ($\bar{x}$) against the standard deviation (s) of the numbers of each species and stage in the samples of each horizontal collection.

tilt, the horizontal distribution is no longer uniform, because of the effects of horizontal convergence, and therefore da/dx is no longer zero. When the thermocline tilt is very small da/dx is only slightly different from zero and equation (5) will be a fairly good approximation to the equation of the concentration gradient,

and can be used to provide a value for a in da/dx (equation 6). Using this an approximation to the required equation can be derived (equation 8) which is only true for small thermocline tilts because of the replacement of a by a_o in equation

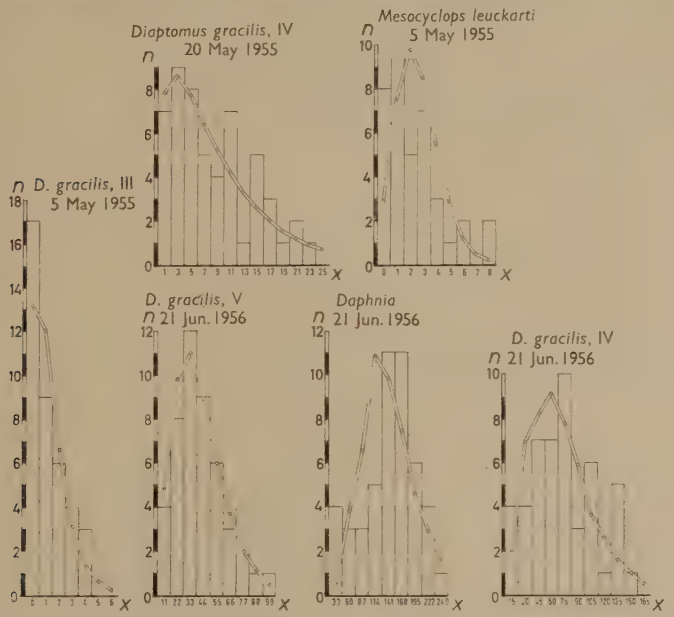

Fig. 13. Histograms of the frequency distribution of the numbers of several species in the horizontal collections of 5 and 20 May 1955 and 21 June 1956 compared with negative binomial series calculated to fit these distributions.

(7) which is necessary for the solution of the equation. Using this argument the required equation may be derived as follows: it is supposed that v_x does not vary with time, therefore from (2)

$$v_x = C \sin x.$$

At the node $X = \frac{1}{2}L$ and $\sin X\pi L^{-1} = \sin x = 1$, therefore $C = v_n$ which is the velocity at the node; therefore

$$v_x = v_n \sin x. \tag{3}$$

Differentiating (3) with respect to x gives

$$dv_x/dx = v_n \cos x. \tag{4}$$

Substituting (4) into (1) and assuming that $da/dx = 0$ gives

$$da/dt = -a\, v_n \cos x,$$

the solution of which is

$$a = K \exp(-tv_n \cos x).$$

At the node $\cos x = 0$; this means that there is no change in concentration, and $K = a_o$, the initial concentration of animals. Therefore

$$a = a_o \exp(-tv_n \cos x). \tag{5}$$

Using (5) to arrive at a value for da/dx gives

$$d/dx\{a_o \exp(-tv_n \cos x)\} = atv_n \sin x. \quad (6)$$

Now (5) is only true when $da/dx = 0$; that is, when $a = a_o$. Substituting into (6) gives

$$da/dx = a_o tv_n \sin x; \quad (7)$$

substituting into (1) from (3) (4) and (7) gives

$$da/dt = -a_o v_n \cos x - a_o t v_n^2 \sin^2 x,$$

the solution of which is

$$a = a_o \exp(-tv_n \cos x) - a_o (\tfrac{1}{2}t^2 + K) v_n^2 \sin^2 x, \quad (8)$$

when $t = 0$, $a = a_o$, and therefore $K = 0$, and

$$a = a_o \exp(-tv_n \cos x) - a_o \tfrac{1}{2}t^2 v_n^2 \sin^2 x.$$

Putting $t = 1$, then $v_n = p_n$, where $p_n = L^{-1}\pi P_n$. (P_n is the horizontal displacement at the node in unit time.) Substituting into (8) gives

$$a = a_o\{\exp(-p_n \cos x) - \tfrac{1}{2}p_n^2 \sin^2 x\}. \quad (9)$$

This equation does not give a complete description of the horizontal distribution of plankton. It is only a very simple beginning and it is advisable to recapitulate the assumptions and simplifications which have been made in deriving it: (a) it is assumed that the animals correct their vertical distributions for displacement by vertical currents; (b) the effects of diffusion have been ignored; (c) the effects of water movements directly induced by wind have been ignored; (d) the effects of vertical migration through the thermocline have been ignored; (e) a part of the interaction between convergence and transport has been ignored; (f) it has been assumed that the two-layered lake model (Mortimer 1952) adequately describes the internal seiches; (g) it has been assumed that the initial distribution of animals is uniform.

Fig. 14 shows graphs of a against x for several values of p_n. The effect of ignoring some of the interaction between convergence and transport is apparent in the curves for $p_n = 0{\cdot}63$ and $p_n = 0{\cdot}79$.

THE EXPLANATION OF THE OBSERVED STATISTICAL PROPERTIES

(*a*) *The linear relationship between the mean and the standard deviation*

Equation (9) shows that the concentration (a) of a species at any point (x) is proportional to the initial concentration (a_o) which is assumed to be uniform. The same is true if several species are present and also the sum of the concentrations of the species is proportional to the sum of the initial concentrations. The numbers of each species in samples taken from this system are Poisson deviates from the expected numbers calculated from equation (9). If the samples are large enough then

$$\bar{a} = p\bar{w}, \quad (10)$$

where p = the proportion of a species in the population,
$\bar{a}$ = the mean number of the species in the samples,
w = number of animals in a sample, and
$\bar{w}$ = the mean number of animals in the samples.

Similarly

$$s_a^2 = n^{-1}\Sigma(pw - p\bar{w})^2,$$
$$s_a^2 = p^2 n^{-1}\Sigma(w - \bar{w})^2,$$
$$S_a = pS_w. \qquad (11)$$

Combining (10) and (11) gives

$$s_w.\bar{w}^{-1} = s_a.\bar{a}^{-1},$$
$$s_a = (s_w.\bar{w}^{-1})\bar{a}.$$

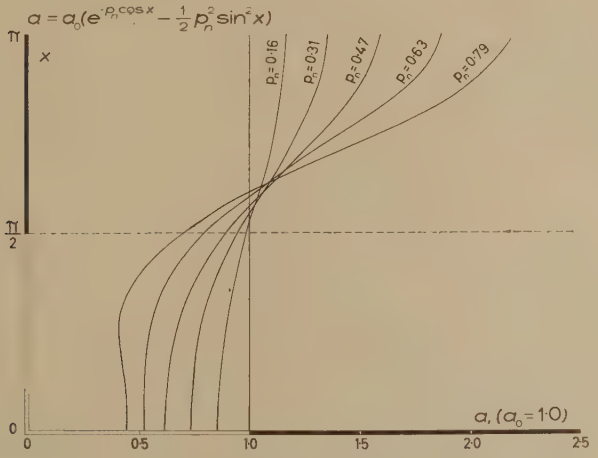

Fig. 14. Graphs of a against x for several values of p_n, where $a_0 = 1$. See text (pp. 231-4) for explanation of symbols.

As p cancels out, the same relationship holds for all the species. This gives a linear relationship between the mean and the standard deviation passing through the origin with a slope depending upon the ratio of the standard deviation to the mean. For small samples equations (10) and (11) are not strictly true, as with decreasing sample size the Poisson distribution becomes asymmetrical. The effect of this on the relationship between the mean and the standard deviation is described below.

(*b*) *The slope of the linear relationship between the mean and the standard deviation*

Using equation (9) sets of values of a for $x = 0°(10°)180°$ and $p_n = 0{\cdot}05\pi$ $(0{\cdot}05\pi)$ $0{\cdot}3\pi$ were calculated. The mean and the standard deviation of the values of a for each value of p_n were calculated. Fig. 15*a* shows a graph of the ratio of the standard deviation to the mean plotted against p_n. Fig. 12 shows that the

slopes of the graphs of mean against standard deviation were usually about 0·5; in Fig. 15*a* a ratio of 0·5 corresponds to a value of p_n of 0·63.

For a uninodal internal seiche in a two layered lake (Mortimer 1952),

$$v_n = \frac{RL^2}{2Th_e},$$

where v_n = the mean nodal velocity in the epilimnion,
R = the slope of the thermocline,
T = the period of oscillation,
h_e = the depth of the thermocline.

This gives $$R = \frac{4Ph_e}{L^2},$$

where $P = p_n L \pi^{-1}$ = the horizontal displacement at the node for a quarter-cycle.

Therefore $$R = \frac{4p_n h_e}{\pi L}.$$

Putting $p_n = 0{\cdot}63$ and putting reasonable values for the north basin of Windermere for h_e and L,

$$R = \frac{4.0{\cdot}63.10}{\pi.6000} = 0{\cdot}001216.$$

The Slape Scar buoy is about 4100 m from the node; therefore a thermocline slope of 0·001216 is equivalent to a thermocline displacement of 5 m or a total swing of 10 m. This is larger than the swings normally recorded by the temperature recorder at the Slape Scar buoy, but it is by no means impossible; several of the swings shown in Fig. 7 are between 10 and 15 m, which is to be expected just after the onset of stratification, when the density difference between the epilimnion and the hypolimnion is small. This calculation implies that, starting with a uniform distribution and assuming that equation (9) gives a full description of the factors producing variations in the horizontal distribution, then a thermocline displacement of 5 m at the Slape Scar buoy is sufficient to produce a distribution with a ratio of standard deviation to mean of 0·5. Bearing in mind the assumptions and simplifications which were made in deriving equation (9), it is considered that a ratio of 0·5 is not inconsistent with the control of horizontal distribution by water movements.

The values of a used to determine the ratio of the standard deviation to the mean describe the concentration gradient along the mid-lake line. The number of animals in samples taken from this gradient at points $x = 0°(10°)180°$ are Poisson deviates from the corresponding values of a. The sum of the Poisson distributions for a given value of a_0 gives a good approximation to the expected frequency distribution of the numbers of animals in samples taken at regularly spaced points along the mid-lake line. Fig. 15*b* is a graph of the mean against the standard deviation of frequency distributions calculated in this way for values of a_0 of 1, 2, 4, 8 and 16 and a value of p_n of 0·63. This shows the effect of the asymmetry of the Poisson distribution on the simplified relationship between the

mean and the standard deviation given by equation 12. Fig. 15*b* is very similar to the observed graphs shown in Fig. 12.

(*c*) *The fit to negative binomial distributions*

Figs. 15 *c-f* show the expected probability distributions of the numbers of animals in samples taken from a distribution described by equation 9 for values of a_o of 2, 4, 8 and 16, for $p_n = 0{\cdot}63$ and $x = 0°(10°)180°$. The figures also show negative binomial distributions which have been fitted to these probability distributions. The fit is quite good except in the middle sections of *e* and *f*; the

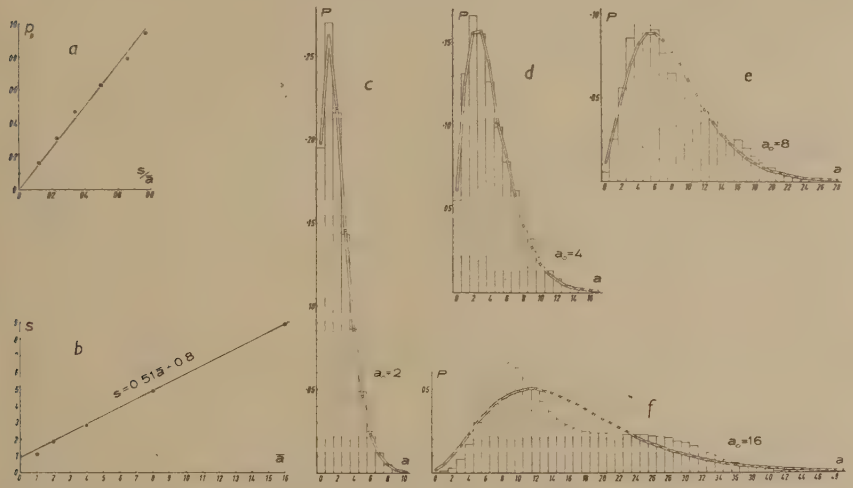

Fig. 15. *a*, a graph of the ratio of the mean to the standard deviation of the curves shown in Fig. 13 plotted against the corresponding value of p_n.
b, a graph of the mean against the standard deviation of samples taken from a distribution described by equation (9) with $p_n = 0{\cdot}63$, $x = 0°(10°)180°$ and $a_o = 1$, 2, 4, 8 and 16.
c-f, histograms of the probability distribution of numbers in samples taken from a distribution described by equation (9) with $p_n = 0{\cdot}63$, $x = 0°(10°)180°$ and $a_o = 2$, 4, 8 and 16; compared with negative binomial distributions calculated to fit these distributions. See text (pp. 231-4) for explanation of symbols.

discrepancies at these points are caused by the approximate nature of equation (9). The statistical properties of the observed distributions can therefore be explained reasonably satisfactorily if it is assumed that they are determined by water movements. It is probable that other explanations of the properties are possible but for the present argument all that matters is that the properties should not be inconsistent with the control of the horizontal distribution by water movements.

DISCUSSION

(*a*) *Application to other lakes*

There is no reason why the principles of the control of the horizontal distribution

of zooplankton by water movements which have been described here should not apply to all stratified lakes. The extent and results of the effect of water movements will vary considerably from lake to lake, depending chiefly on the size and shape of the lake. Water movements probably have the greatest effect on the horizontal distribution of zooplankton in lakes of about the size of the north basin of Windermere with a seiche period of about 12 h. If diurnal vertical migration through the thermocline occurs, then in lakes of this size there may be only one migration during each swing of the thermocline. In larger lakes, with a seiche period of several days, there will be several migrations during each swing of the thermocline and the change in distribution produced when the animals are in the epilimnion will be reversed when they are in the hypolimnion. In small lakes with a short seiche period there may be several oscillations of the thermocline between each diurnal vertical migration, and the results may be similar to those in Windermere. Many lakes of this size are too shallow to be thermally stratified, and if they are, there may be considerable oxygen depletion in the hypolimnion which prevents vertical migration through the thermocline, and only the temporary effects associated with an internal seiche will occur. In very large lakes it is probable that the effects of internal seiches will be masked by other factors such as standing currents or biological variations in space and time.

(*b*) *Census sampling of the zooplankton in Windermere*

The distribution of the zooplankton in Windermere is highly non-random in both the horizontal and the vertical planes. The variability in the vertical plane can easily be eliminated in samples by taking vertical hauls from the bottom to the surface of the lake. Horizontal variation is not so easily disposed of; it may ultimately be possible to derive an accurate equation describing the horizontal distribution of the plankton in terms of water movements, and to use this equation to calculate the abundances using the counts of a single vertical haul. At the moment this is impracticable, and in any case it would require extensive measurements of temperature or current speeds to obtain values for the water movement terms of the equation. There are several other possibilities. The variability in the horizontal plane can be calculated by taking a large number of vertical hauls over the whole area of the lake in as short a time as possible. It can also be calculated, slightly less satisfactorily but possibly more conveniently, by taking a large number of vertical hauls at regular intervals of time, which must be short compared with the seiche period, at a single station situated near one end of the basin. Estimates of abundances and the accuracies of the estimates can be calculated from these sets of samples. Another method which would probably give a very good estimate of abundance but with unknown accuracy is to extrapolate from a small number of vertical hauls, using the results of a continuous horizontal collection made at night and covering as much of the area of the lake as possible.

ACKNOWLEDGMENTS

I am indebted to Mr H. C. Gilson for allowing me to make use of the facilities of the Freshwater Biological Association's Windermere laboratory and for permission to publish the wind and temperature data. The wind data for Sellafield were supplied by the Atomic Energy Authority. I am grateful to Dr C. H. Mortimer for many useful discussions. I must also acknowledge the assistance of many members of the laboratory staff especially Mr G. J. Thompson, Mr W. C. Findley who made the sampling apparatus, and Messrs K. Shepherd and F. Prickett, the crew of the launch *MYSIS*.

The work was carried out while I was receiving a grant from the Nature Conservancy and an extended account of the work has been submitted to the University of London as a thesis for the degree of Ph.D.

SUMMARY

1. A continuous horizontal plankton sampler and a vertical closing net were used for making collections of the zooplankton of the north basin of Windermere. The horizontal sampler was carried in a motor launch and consisted of a pump and hose, collecting continuously at a depth of 4·5 m, and two filter chambers, which were operated alternately at regular intervals as the launch travelled through the water.

2. Temperature and wind data were used to assess the nature of the water movements at the times of the collections. It is concluded that the horizontal distribution of the zooplankton is determined to a large extent by the water movements.

3. A theoretical consideration of the effects of water movements in a stratified lake on the horizontal distribution of zooplankton indicates that an internal seiche should have a temporary effect on the distribution, while the effect of wind and of an internal seiche combined with diurnal vertical migration through the thermocline should have a permanent effect on the horizontal distribution.

4. An approximate equation describing the horizontal distribution of zooplankton during an internal seiche is derived. This equation is used to show that certain statistical properties of the observed distributions may be determined by the effects of water movements.

5. It is considered that the principles of the control of the horizontal distribution of zooplankton by water movements should apply to all thermally stratified lakes, but that in lakes much larger than Windermere these effects may not be very great and may be obscured by other factors.

6. Several methods of census sampling of the zooplankton of Windermere are described, all of them rather complicated and laborious. A method which should yield reasonable estimates for not too much labour is to take a fairly small number of bottom to surface vertical hauls at different stations and to extrapolate from these, using the results of a continuous horizontal collection taken at night and covering as much of the area of the lake as possible.

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SOME OBSERVATIONS OF ZOOPLANKTON SWARMS IN WINDERMERE

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The number of recorded direct observations of swarms of zooplankton in lakes appears to be very small. Birge (1897) observed swarms of *Daphnia hyalina* Sars. on three occasions; they were fairly distinct patches, differing in size but measuring tens of metres. The animals were confined to a narrow depth zone of only a few centimetres at the surface of the water. The concentrations were high, about 1000 per litre, and the animals were nearly all adults. Birge considered that swarms of this type were not very common and were only found during very calm conditions. *Daphnia* has been observed to be very patchy in its distribution (Ragotzkie & Bryson 1953, Southern & Gardiner 1926) but I have not been able to find any other references describing swarms of the type observed by Birge.

In the evening of 24 June 1955 a small swarm of *D. hyalina* was seen in Mitchell Wyke, a deep, sheltered, roughly semi-circular bay in Windermere. The swarm was fairly distinct, about 1 m in diameter and confined to the top 10 cm of the water; the distribution in the surrounding area showed scattered patches of animals, which were not confined to the surface but occurred at varying depths down to about 50 cm. A number of samples were taken using a dip jar, one from the *Daphnia* swarm, four from the surrounding patches and eight at random. The results expressed in numbers per litre are given in Table 1. The *Daphnia* swarm

Table 1. *Dip jar samples, Mitchell Wyke, 24 June 1955*

The figures are numbers per litre.

	Daphnia swarm	Selected samples				Random samples							
Diaptomus ♀	0	0	5	0	0	3	0	5	0	0	0	0	3
Diaptomus ♂	0	49	56	8	72	8	3	3	0	5	18	5	0
Mesocyclops	0	0	8	0	3	0	3	5	0	0	3	0	3
Daphnia	9100	89	205	72	338	44	15	8	0	46	49	28	3
Bosmina	383	5	5	8	10	5	0	38	3	5	13	8	3

was obviously of the same type as those observed by Birge, even though the size was smaller and the concentration was much higher. *Bosmina obtusirostris* Sars. was concentrated in the *Daphnia* swarm but not in the surrounding patches, which contained *Daphnia* and adult male *Diaptomus gracilis* Sars.

Table 2 gives instar analyses for *Daphnia* from the swarm and from a collection made in the open water of the lake on the following evening. The swarm contained a much higher percentage of stage II than the open water sample.

On the night of 13 July 1955 a series of dip jar samples was taken in the open water of the lake, and direct observations were made with a torch shining into the water. Absolutely calm conditions are required for this type of observation. A clear swarm pattern was observed for what was subsequently found to be adult male *Diaptomus gracilis*. It occurred in groups of patches, each patch only a few

Table 2. *Instar analyses of* Daphnia, *24–25 June 1955*

	24 June Swarm (%)	25 June Open water (%)
Stage I	4·0	2·5
Stage II	82·0	37·0
Stage III	13·5	21·5
Stage IV	0·5	10·5
Adult	0·0	29·0

centimetres across and each group probably several metres across, but the boundaries were very diffuse and it was difficult to judge their size. Table 3 gives the results of the sampling: samples *g*, *j* and *k* show clear concentrations of adult male *D. gracilis*. July 1955 was a mating period for *D. gracilis* and it seems possible that these were mating swarms.

Table 3. *Dip jar samples, Windermere, 13 July 1955*

The figures are numbers per litre

	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	*k*	*l*	*m*	*n*	*o*
Daphnia	1	2	1	0	0	0	0	0	0	0	0	1	0	0	0
Diaptomus ♂	1	0	0	0	2	12	53	4	17	63	35	7	6	1	1

There are two obvious factors which might produce and maintain plankton swarms of the types described above: turbulence and social activity of some kind implying purposeful movements by the animals. It seems likely that some social activity is involved, the composition of the *Daphnia* swarm and the possibility that the swarms of adult male *Diaptomus gracilis* were mating swarms suggests this; turbulence might be expected to be less discriminating. On the other hand the patches around the *Daphnia* swarm contained *Daphnia* and adult male *Diaptomus gracilis*. This might result from a combination of both factors, turbulence initiating the swarms, which were then enlarged and maintained by social activity.

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THE DISTRIBUTION AND SUBSEQUENT DISAPPEARANCE OF SHEEP DUNG ON PENNINE MOORLAND

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In the course of work on dung-feeding Coleoptera (White, in press) data were collected on the amount of dung deposited by sheep on certain types of moorland vegetation. The addition of dung and the mode of its incorporation in the soil is of importance when discussing problems of plant and animal production from upland areas. The general aspects of utilizing moorland, bog and similar areas have been considered by Darling (1955), Pearsall (1950), Hughes (1955), and Cragg (1958). In this paper, attention will be concentrated on the amount of dung produced, and the climatic and biological factors responsible for its subsequent disappearance and utilization.

Table 1. *The major vegetation types and the numbers of sheep on the study area*

Vegetation types			Numbers of sheep					
			1956		1958			Average density (no./100 ha)
	Area (hectares)	% total area	17 July	28 Aug.	8 July	15 July	1 Sept.	
Grassland	26	14	–	–	27	29	66	157
Juncus squarrosus moor	19	10	–	–	12	15	31	102
Calluna and *Eriophorum* moor	120	65	–	–	17	25	50	25
Remainder (largely *Juncus effusus*)	20	11	–	–	17	10	32	98
Total	185		203	278	73	79	179	

The observations were made during 1956 and 1958 on the Moor House National Nature Reserve (Conway 1955). Sampling sites were scattered over an area of approximately 185 hectares in parts of the valleys of Troutbeck, Moss Burn and Roughsyke. The area included three main types of vegetation in the proportions shown in Table 1.

METHODS

Thirty sample sites each of 100 m^2, were established on grassland, *Juncus squarrosus* moor, and *Calluna* and *Eriophorum* moor. Dung was examined at regular intervals on these sample sites in 1956 and on two occasions in 1958. The presence of lumbricid worms, dipterous larvae and *Aphodius* adults and larvae was noted on most occasions. By examination of the dung it was usually possible to identify the previous occupants. Dipterous larvae leave a dropping with part

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of it perforated by many closely-set borings. *Aphodius* adults produced broader irregular tunnels, while their larvae produced characteristic spherical cavities. Lumbricidae tunnelled in dung rather like *Aphodius*, but also removed dung from the under-surface.

THE DISTRIBUTION OF SHEEP AND THEIR DUNG

Sheep were present on the area from mid-April to early November. In that time, they were left very much to themselves, being shepherded only for shearing, castration and removal for the winter. Thus, the distribution of animals on the area probably indicated the sheep's preference for particular localities and vegetation types. The lower numbers of sheep in 1958 (Table 1) resulted from one farm having only 150 ewes and followers on the moor, whereas in 1956 the number was nearer 1000. The table also indicates that the density of sheep on different vegetation types varied considerably. For this reason, the distribution of dung was expected to vary on different plant communities. Table 2 shows this to be the

Table 2. *The amount of dung deposited compared with sheep density, on various types of vegetation*

Vegetation type	Dung deposited in 1956 (cm^3/m^2)	Density of sheep in 1958 (no./100 ha)	Ratios	
			Dung	Sheep
Grassland	119	157	6	6
J. squarrosus moor	78	102	4	4
Calluna and *Eriophorum* moor	18	25	1	1

case. Estimates of the average amount of dung deposited in a year on 1 m^2 of each vegetation type were proportionately similar to sheep density.

The sample sites covered the full range of grassland available, from sites with quite luscious growth of *Agrostis* and *Deschampsia*, to areas with *Nardus* and *Festuca* barely forming a complete turf. The distribution of dung on the thirty grassland sites was not random, those with better grass growth having more dung deposited upon them ($P<0{\cdot}001$ for all vegetation types). *Nardus* is a grass known to have low mineral requirements, and where it was found commonly the number of droppings was low (Table 3). Similarly, on sites where there was only a turf without a well-defined soil layer beneath, small numbers of droppings were found. Thus, low numbers of sheep droppings were found where the soil mineral supply was poor and were probably directly related to the grazing potential of such areas. On sites where the xerophytic lichen *Cladonia* was abundant, only small numbers of droppings were found. Droppings on *Juncus squarrosus* moor, and *Calluna* and *Eriophorum* moor were also distributed non-randomly. The explanation of this may be largely nutritional, as on grassland, but no evidence of this was obtained. The use of some of the sample sites as resting places certainly accounted for some of the aggregation of droppings on these vegetations.

THE REMOVAL OF SHEEP DUNG FROM THE SOIL SURFACE

The removal of dung in winter was largely effected by wind, rain, snow and ice, for the climatic conditions in the area are sufficiently severe to reduce animal activity to a minimum at this time. Table 4 shows the size distribution of droppings examined in April, all of which had overwintered. It is suggested that the high proportion of very small droppings on grassland was the result of more severe erosion there, for the short turf afforded less protection from the elements than the taller growth of *Juncus*, *Calluna* and *Eriophorum*. The table also shows the mean dropping sizes late in the year compared with the means for overwintered dung. Even if it is assumed that no droppings have disappeared completely, it can be seen that 30-50% of the dung was removed during the winter.

Consideration was given to three of the invertebrate groups which use dung: Lumbricidae, the larvae of dipterous flies, and the adults and larvae of the beetles of the genus *Aphodius*. Infestation of sheep dung by these organisms reaches high proportions occasionally. Dipterous larvae were found in over 50% of droppings on several occasions, while in May 1956 over 70% of recent droppings were infested

Table 3. *Association of dropping numbers with vegetation and soil conditions on grassland*

		Number of droppings		χ^2	P
		observed	expected		
Mineral content of soil indicated by *Nardus*	present	2518	3290	25	0·001
	absent	2964	2192		
Depth of soil	turf only	1308	1826	22	0·001
	soil and turf	4174	3656		
Liability of soil to drought indicated by *Cladonia*	present	1940	2375	13	0·001
	absent	3542	3107		

by adult *Aphodius* beetles. Dr J. A. Svendsen (personal communication) recorded that at Moor House in August 1953 34% of droppings on grassland contained Lumbricidae. These three groups of animals remove considerable amounts of dung and by their tunnelling activities, make it suitable for habitation by other Coleoptera, Collembola, Acarina and other organisms. The infestation of dung by worms, fly larvae and *Aphodius*, in July and August 1958, is shown in Table 5.

Seasonal variation in numbers and activity of the major dung removers is reflected in the infestations found in sheep dung. White (in press) showed that the numbers of *Aphodius* adults in dung decreased as the summer progressed, and Table 6 shows that the percentage infestation of droppings by *Aphodius* was also less later in the summer. On the other hand Lumbrididae were more commonly found in dung in August than in July, but the percentage infestation by dipterous larvae did not differ in July and August. The most common dipterous inhabitant of dung was *Scopeuma*, others of importance were several species of Sphaeroceridae. Table 6 also shows that both flies and beetles infested droppings irrespective of the type of vegetation on which the dung was found. This was not unexpected, since these animals reached the dung by flying. The infestation of

Table 4. *The removal of dung by climatic factors in winter*

Sheep droppings deposited in 1955, and examined in April 1956.

	Total droppings	Per cent of droppings in each size-group					Mean dropping size Apr. 1956 (cm^3)	Mean dropping size deposited Oct.–Nov. 1955 (cm^3)	Estimate of percentage removed
		0–25	26–50	51–75	76–100	>100 ccs			
Grassland	603	55	36	6	2	1	28	75	49
Juncus squarrosus moor	883	25	49	18	6	5	41	75	45
Calluna and *Eriophorum* moor	248	21	46	18	10	8	52	80	35

Table 5. *Infestation of dung by Lumbricidae, Diptera and* Aphodius *in July and August 1958*

			Grassland (1500 m²)		*Juncus squarrosus* moor (1500 m²)		*Calluna* and *Eriophorum* moor (3000 m²)	
July 1958			No.	%	No.	%	No.	%
Less than 2 weeks old	Not infested		28	–	15	–	4	–
	Infested on examination	Lumbricidae	0	0	2	4	4	25
		Diptera	28	38	27	54	7	44
		Aphodius	36	49	21	42	5	31
	Never infested		6	–	4	–	1	–
	Infested at some time	Lumbricidae	2	3	4	8	6	38
		Diptera	41	56	33	66	9	56
		Aphodius	55	75	34	68	8	50
	Total droppings		73	–	50	–	16	–
More than 2 weeks old	Not infested		64	–	55	–	20	–
	Infested on examination	Lumbricidae	2	2	1	1	1	4
		Diptera	24	23	30	30	1	4
		Aphodius	24	23	22	22	2	8
	Never infested		7	–	14	–	4	–
	Infested at some time	Lumbricidae	35	34	16	16	2	8
		Diptera	63	60	68	68	15	94
		Aphodius	54	51	35	35	9	38
	Total droppings		107	–	100	–	24	–
August 1958								
Less than 2 weeks old	Not infested		45	–	13	–	8	–
	Infested on examination	Lumbricidae	8	7	2	4	1	3
		Diptera	60	53	31	66	24	70
		Aphodius	34	30	8	17	13	17
	Never infested		38	–	11	–	3	–
	Infested at some time	Lumbricidae	17	15	3	6	4	12
		Diptera	60	53	32	68	27	81
		Aphodius	42	37	8	17	19	55
	Total droppings		114	–	47	–	35	–
More than 2 weeks old	Not infested		58	–	45	–	21	
	Infested on examination	Lumbricidae	12	11	5	8	1	3
		Diptera	32	29	9	14	9	28
		Aphodius	21	19	5	8	5	16
	Never infested		16		13	–	3	
	Infested at some time	Lumbricidae	52	47	17	27	6	18
		Diptera	77	70	43	68	23	71
		Aphodius	37	34	10	16	7	22
	Total droppings		110		63	–	29	

Table 6. *Infestation of dung by* Aphodius, *Lumbricidae and Diptera*

		Number of droppings: Infested at some time	Number of droppings: Total	Per cent infested	P	Data used
Aphodius	July	195	370	53	< ·01	All dung
	August	123	398	31	(1 d.f.)	
Lumbricidae	July	53	231	23	< ·01	Dung more than 2 weeks old on all vegetation types
	August	75	202	35	(1 d.f.)	
Diptera	July	229	370	62	·20	All dung
	August	262	398	66	(1 d.f.)	
Diptera	Grassland	241	404	60		All dung which was examined in July and August 1958
	Juncus squarrosus moor	166	260	64	·0·3	
	Calluna and *Eriophorum* moor	74	104	71		
Aphodius	Grassland	70	187	37		All dung which was less than 2 weeks old on examination in July and August 1958
	Juncus squarrosus moor	29	97	38	·0·3	
	Calluna and *Eriophorum* moor	18	51	35		
Aphodius	Grassland	636	3544	18		All dung examined at 4-weekly intervals from April-November 1956
	Juncus squarrosus moor	133	823	16	·0·3	
	Calluna and *Eriophorum* moor	46	287	16		
Lumbricidae	Grassland	87	217	66		Dung examined in July and August which was between 2 and 4 weeks old
	J. squarrosus moor	33	163	49	< ·001	
	Calluna and *Eriophorum* moor	8	53	16		
Lumbricidae	Grassland	27	30	90		Dung which was at least 3 months old on examination in September 1956
	J. squarrosus moor	43	61	71		
	Calluna and *Eriophorum* moor	37	58	63		

dung by worms did vary with the vegetation type, these animals being most active on grassland and least active on *Calluna* and *Eriophorum* moor. The infestation of dung by Lumbricidae differed conspicously in one other respect from *Aphodius* and dipterous infestations. Observation showed that for the latter two groups, infestation had to be effected within a few days of the dropping being deposited, while in the case of worms, infestation rarely occurred before the dung was 2 weeks old. Table 6 shows that the majority of droppings more than 3 months old had been attacked by worms at some time. Thus dung several months old is still suitable as food for worms, which suggests that if dung remains long enough and there are worms available to feed on it, then most, if not all, droppings will be attacked eventually.

The infestations described above indicate the activity of biotic agents in dung, but no measure was available of the actual amounts of dung removed or of the biomass of organisms effecting the removal. Estimates of the average duration of dung on various vegetations revealed marked differences. It has been shown that dipterous larvae and *Aphodius* beetles attack dung irrespective of the vegetation type, so the differences shown in Table 7 are probably related to the feeding activities of Lumbricidae and to different erosion intensity exerted by the physical

Table 7. *The average duration of droppings on several vegetation types*

	Droppings deposited 1956	Droppings overwintered on same area	Average duration (days)
Grassland	5482	603	39
Juncus squarrosus moor	3156	549	64
Calluna and *Eriophorum* moor	633	249	143

environment. In the summer of 1956, the removal of dung by worms was compared on grassland and *Eriophorum* moor. Fresh dung in 100 cm^3 amounts was laid out on both types of vegetation in early June. The weather conditions were unfavourable for insect activity with the result that infestation by Diptera and *Aphodius* was slight. The dung was examined after 60 days, when 50% had disappeared from grassland and only 9% from *Eriophorum* moor. The change in volume of the dung was almost entirely attributable to the activities of the worms.

DISCUSSION

The vegetation types studied provided variable grazing for sheep, and as a result the density of dung also varied. On grassland, *Juncus squarrosus* moor, and *Calluna* and *Eriophorum* moor, the amounts of dung varied in the ratios 6 : 4 : 1 respectively. The effects of biological and physical factors in removing dung also varied among the vegetation types. The average duration of sheep droppings was longest on *Calluna* and *Eriophorum* moor and shortest on grassland. Thus, the cycle started by the sheep involved the turnover of more material per unit area on grassland than on *Calluna* and *Eriophorum* moor, and the turnover of such

materials as faeces was considerably slower on those vegetation types which produced less fodder.

The percentage infestation of droppings by the first organisms in the dung succession, the dipterous larvae and *Aphodius* adults, was similar on all vegetation types. Thus the differences in average duration of droppings largely resulted from the variable erosion effects and different intensity of activity on the part of the Lumbricidae. The worms spread their activity over a longer period than flies and beetles, and thus are responsible for the destruction of material remaining after the initial colonizers have left the dung. Because dung is only attractive to flies and beetles for several days, bad weather conditions may prevent them from colonizing it. Under these conditions its destruction is carried out by Lumbricidae and physical factors. Even though flies and beetles infested dung to a similar extent on all vegetation types, they were relatively most important in rapidly utilizing dung on *Calluna* and *Eriophorum* moor, where the removal of dung by worms was slow because of their low numbers.

Wind and precipitation have been shown to remove at least 30-50% of dung during winter months when animal activity is at a minimum. The ultimate removal of dung from the soil surface rests largely with the physical environment, for no time limit is set upon the action of the elements.

ACKNOWLEDGMENTS

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SUMMARY

1. On Pennine moorland the density of dung deposited on grassland, *J. squarrosus* moor, and *Calluna* and *Eriophorum* moor, was in the ratio 6 : 4 : 1.

2. Factors of the physical environment were most effective in the removal of dung from the soil surface.

3. Lumbricid worms were the most effective biological agents removing dung; dipterous larvae and *Aphodius* beetles were relatively unimportant.

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A STUDY OF THE MORTALITY OF THE STARLING BASED ON RINGING RECOVERIES

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(With 6 Figures in the Text)

In Great Britain, there have been more starlings (*Sturnus vulgaris*) ringed and recovered* than any other bird. Over 207 000 starlings had been ringed by the end of 1957 and the number ringed each year continues to increase. The total number of recoveries in this period was 7541 and this total is now increasing by nearly a thousand a year. The only analysis of the mortality of the starling in Great Britain is that of Lack (1943) who used data from the beginning of the ringing scheme in 1909 to the end of 1934. Since then there have been many more recoveries, and Haldane (1955) has published a method for calculating mortalities which allows recent recoveries to be used, although some of the ringed birds may be still alive.

Lack & Schifferli (1947) re-analysed the data of Lack (1943) and showed that the starling had an average annual mortality of 52% in Great Britain while it has a mortality of 63% in Switzerland. Kluijver (1935) determined the mortality of the starling in Holland by recording the survival of marked breeding birds in subsequent years and obtained a value of 50% mortality each year. The mortality of the European starling in north-east United States and Canada has been estimated as 50% (based on the recovery of 205 birds ringed as nestlings) and 57·5% for starlings of unknown age, but more than 6 months old (Kessel 1957). More recently Davis (1959) has claimed that the average annual adult mortality of male starlings in the U.S.A. is 56% while that of the females is 70%. These values were derived from the adult: first-year ratio in March. However, this method is only applicable if all of the first-year birds breed in their first year. This is not so in the starling, as has been shown by the work of Kluijver (1935), Bullough (1942) and Kessel (1957), and this estimate therefore probably gives an exaggerated measure of the adult mortality. This criticism does not detract from the fact that Davis has demonstrated that the male and female starlings suffer a differential mortality.

The large number of starlings ringed each year in Great Britain makes it possible to estimate the annual mortality for individual years, and a preliminary analysis is presented in this paper. In addition, regional mortality is examined and extended to starlings of foreign origin wintering in this country. It has been held that the mortality-rate of passerines is independent of age after the first few

* In this paper the term 'recovery' applies to birds which were dead or dying at the time of recovery. Birds which have been recaptured and released again have not been included in the analysis. A number of recoveries has been omitted because the date was not reported with sufficient accuracy.

months of life (Farner 1945, Lack 1946) and the applicability of this hypothesis to the starling has been examined.

VALIDITY OF RINGING RECOVERIES IN MORTALITY STUDIES

Of all starlings ringed, only about 3·6% are recovered as dead or as dying birds. To use these recoveries to estimate mortality, it is essential that they are a fully representative sample of the age-groups present in the population. If, for example, cats killed proportionately more young starlings than were in the population (*e.g.* because the young birds were less wary), then these recoveries would give an excessively high mortality-rate. Furthermore, ring loss could also affect the estimate of the mortality-rate, since this is more likely to occur amongst old birds and would give too few recoveries amongst the older age-groups. A third possible source of error is that which could be produced by foreign bred starlings being ringed and recovered in Great Britain. If they were not recognized as foreign birds and had a different mortality-rate from the British population, then they could bias the numbers recovered in each year-group. These possible causes of error will be discussed below.

(*a*) *Wear and loss of rings*

Doubt has recently been cast upon the validity of ringing recoveries as a means of estimating the mortality of sea-birds. Coulson & White (1957) examined data published by Lack (1943) on the ringing recoveries of the black-headed gull (*Larus ridibundus*) and confirmed that a significantly greater proportion of these gulls were recovered 'shot' during their first year, but this did not apply to the recoveries of the shag (*Phalacrocorax aristotelis*). Lack (1943) also showed that ringing recoveries gave an excessively high estimate of the annual mortality of the lesser black-backed gull (*Larus fuscus*), the cormorant (*Phalacrocorax carbo*) and the black-headed gull (*Larus ridibundus*). Coulson & White (1955, 1957, 1959) have shown that this also applies to ringing recoveries of the kittiwake (*Rissa tridactyla*) and the shag. They attribute this error in these two species to the abrasion and eventual loss of rings which have been on the birds for as little as 3 years. These excessively high estimates of the adult mortality of sea-birds, based on ringing recoveries, do not appear to apply so extensively to the passerines. Several of the mortality estimates derived from ringing recoveries agree with those dependent on other methods (Lack 1954, pp. 91-2).

Some loss of rings does occur amongst starlings. One ring was returned having fallen from the sky and landed at the feet of the finder, while another ring was found in a bird bath. Mr R. Spencer (Ringing Officer of the British Trust for Ornithology ringing scheme), informs me that, after a number of years, the aluminium rings tend to gape on starlings and become worn, particularly on the inside. One ring which was returned after 7 years showed distinct signs of wear, although the inscription and numbers were still legible. The indications are that loss of rings from starlings is small.

(b) Bias due to selective mortality

Approximately 67% of the ringing recoveries of the starling are simply reported as being 'found dead', with no information as to the cause of death. The remaining 33% give some information concerning the cause of death. Of these, 15% are birds reported as having been 'shot', presumably by air-guns as well as by shot-guns and rifles. The next most frequent group, 11%, are those which are recorded as captured or killed by cats. The birds carried by cats are probably alive when first caught, but it is not known whether these birds were ill or injured before capture. Other recorded causes of mortality are: falling down chimneys (3·0%), drowned (1·4%), killed by other predators (dogs, stoat, fox, hawks and owls) (1·4%), killed by road traffic (0·6%), and killed by flying into telephone wires (0·6%). Obviously these proportions do not represent the actual proportions killed. A bird killed by a cat is much more likely to come to the attention of man than one killed by a hawk or an owl. Likewise ringed starlings which fall down a

Table 1. *Estimates of the average annual adult mortality according to cause of death*

Ringing recoveries of starlings ringed before 1950 and of unknown age.

	Survival after ringing (year-groups)										Total	Average annual mortality (%)
	1	2	3	4	5	6	7	8	9	10		
'Found dead'	482	233	101	57	26	14	9	1	1	1	925	51·1 ± 1·2
Cat	57	26	19	8	2	2	1	1	0	0	116	49·4 ± 3·3
Shot	157	50	27	11	4	2	1	0	0	0	252	59·8 ± 2·4
Falling down chimney	22	9	5	4	1	0	0	0	0	0	41	54 ± 5·7
Other predators	12	4	1	2	0	1	0	0	0	0	20	54 ± 8·1
Other miscellaneous causes	7	15	4	3	0	0	0	1	0	0	30	
Total	737	337	157	85	33	19	11	3	1	1	1384	52·8 ± 1·0

chimney are very likely to produce a recovery and the same applies to birds which have been shot. Starlings killed by flying into telephone wires are only so described if the accidents are seen.

To examine the variability of mortality estimates due to different causes of recovery, an analysis was made using starlings which survived after 1 January after ringing and which had been ringed before 1950. The recoveries are grouped according to cause of mortality and the age after ringing at which death took place. The results are shown in Table 1 and also Fig. 1 and suggest that only those recorded as having been shot differed markedly from those which were 'found dead'. A further analysis using the additional 'incomplete' recoveries from 1950 to 1957 (Table 2) and employing the method suggested by Haldane (1955) established the difference as being significant ($P<0·01$) between those which were shot and found dead, while the difference for birds killed by cats and found dead was not significant. Fig. 1 shows that the birds recovered as being shot, killed by cats and found dead have a constant mortality-rate irrespective of age and this can be

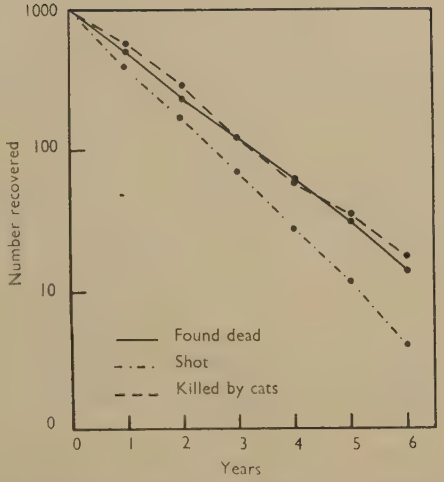

Fig. 1. A comparison of the survival of starlings which are recovered as 'found dead', shot and killed by cats. Each group started with 1000 birds alive. The slope of the graph indicates the mortality-rate (log scale).

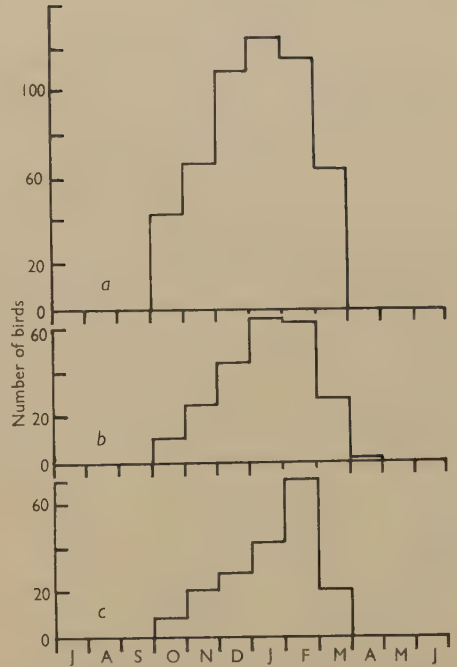

Fig. 2. The month of ringing of starlings subsequently recovered on the continent of Europe: *a*, in Belgium, Holland and Germany; *b*, in Norway, Sweden and Denmark; *c*, in Russia, Finland and Poland. The last group apparently arrive later.

confirmed statistically. This would not be expected if young birds were more liable to be shot; then the mortality-rate would decrease after the first year. A possible explanation of this different mortality-rate of starlings which have been shot is that the mortality is greatest in areas where shooting is most likely (*e.g.*

Table 2. *Numbers of adult starlings recovered*

Year of ringing		Survival after ringing year-groups										Total	Average annual mortality (%)
		1	2	3	4	5	6	7	8	9	10		
FOUND DEAD													
Before	1950	482	233	101	57	26	14	9	1	1	1	925	
	1950	17	7	1	2	1	1	0	1			30	
	1951	10	7	7	2	3	0	1				30	
	1952	27	8	5	2	0	7					49	
	1953	30	20	10	6	7						73	
	1954	56	27	13	10							106	
	1955	90	73	28								191	
	1956	87	59									146	
	1957	126										126	
Total	1950-7	443	201	64	22	11	8	1	1	0	0	751	48·7 ± 1·0
SHOT													
Before	1950	157	50	27	11	4	2	1	0	0	0	252	
	1950	0	1	0	1	0	0	0	0			2	
	1951	2	1	0	0	0	0	0				3	
	1952	3	2	1	0	0	0					6	
	1953	4	4	2	1	0						11	
	1954	5	4	2	1							12	
	1955	11	6	3								20	
	1956	5	9									14	
	1957	23										23	
Total	1950-7	53	27	8	3	0	0	0	0	0	0	91	57·7 ± 2·0
KILLED BY CATS													
Before	1950	57	26	19	8	2	2	1	1	0	0	116	
	1950	5	1	0	0	1	0	0	0			7	
	1951	1	2	0	0	0	0	1				4	
	1952	7	3	1	0	0	1					12	
	1953	5	0	0	1	1						7	
	1954	20	7	11	5							43	
	1955	20	9	8								37	
	1956	23	15									38	
	1957	26										26	
Total	1950-7	107	37	20	6	2	1	1	0	0	0	174	46·6 ± 2·5

the fruit growing areas of south-east and south-west Britain) and the increased mortality may represent the effectiveness of this shooting.

(*c*) *Bias due to foreign birds wintering in Great Britain*

The period spent in Great Britain by starlings which were subsequently recovered abroad in the breeding season has been determined by grouping the month of ringing according to the area of recovery (Fig. 2). Only one starling of those ringed in Britain as adults between April and September inclusive, was

recovered abroad, while many foreign starlings were present in this country from October to March inclusive. Note the apparent later arrival of starlings from Russia, Poland and Finland in relation to others from western Europe. If any of these foreign birds come from populations which have a different mortality-rate, then they may bias the mortality estimates of the British starling. The extent of this error can be determined in two ways.

The mortality-rates of starlings of known British origin and of birds which were mixed with foreign starlings can be compared. Thus starlings ringed in Great Britain between April and September were of British origin as were birds ringed from October to March and which were recovered in Great Britain between April and September. This only left those starlings ringed between October and March and recovered between the same months in Great Britain which were likely to contain birds born outside Great Britain. The two groups gave identical mortality-rates suggesting that the bias from foreign starlings does not influence the estimate of the mortality-rate.

The second method was to estimate the mortality-rates of starlings which had wintered in Great Britain and had been recovered between April and September on the Continent. These results are given in Table 3 and indicate that there was little difference in the mortality-rates of starlings of foreign origin which winter in Great Britain. Thus this possible source of bias can be excluded.

Considering the information available, there is no justification in excluding any of the recoveries on the grounds of being biased, and the average annual adult mortality of $52{\cdot}8\% \pm 1{\cdot}0\%$ can be taken as being the best estimate.

(*d*) *Bias due to disproportionate ringing in urban areas*

It is likely that a higher proportion of starlings are ringed in urban and suburban areas than in rural areas. Thus the presence of a different mortality-rate in rural areas (if such exists), will not be fully represented in the average estimates. This possible source of error may not be of great importance in the starling, which is mainly restricted to human habitation, but is likely to be of more importance in species which occur commonly in both suburban and rural areas, such as the blackbird (*Turdus merula*). At present the relationship between different types of environment and the adult mortality have not been fully examined. It is not possible to carry out such an analysis from ringing recoveries since the type of environment is not usually recorded at the time of recovery.

ANNUAL MORTALITY OF STARLINGS OF KNOWN AGE

The data used were restricted to starlings which had been ringed as young or as juveniles before their first 1 August of life. Lack's (1943) data have been included since they incorporate additional recoveries from the Aberdeen University ringing scheme and give a larger sample. B.T.O. recoveries up to and including 1949 have been utilized. The results are shown in Table 4. It can be seen both from inspection and from statistical treatment, that after the first 1 August of

Table 3. *Numbers of starlings ringed in Great Britain and recovered dead from April to September in various countries*

Winter of ringing	Survival after ringing (year-groups)										Total	Average animal mortality (%)
HOLLAND AND BELGIUM	1	2	3	4	5	6	7	8	9	10		
Before 1949-50	24	9	2	2	2	1	1	1	0	0	42	
1949-50	2	1	0	0	0	0	0	0	0		3	
1950-1	4	1	0	1	0	0	0	0			6	
1951-2	10	5	3	2	0	1	0				21	
1952-3	7	3	1	0	0	1					12	
1953-4	11	4	4	1	0						20	
1954-5	14	4	1	1							20	
1955-6	5	10	3								18	
1956-7	10	2									12	
1957-8	11										11	
Total 1949-58	74	30	12	5	0	2	0	0	0		123	50·8 ± 3·5
GERMANY												
Before 1949-50	41	23	9	6	3	0	0	1	1	0	84	
1949-50	1	1	0	0	0	0	0	0	0		2	
1950-1	7	3	0	0	0	0	0	0			10	
1951-2	7	13	1	1	0	0	0				22	
1952-3	6	2	1	0	0	0					9	
1953-4	11	6	0	0	0						17	
1954-5	4	5	1	1							11	
1955-6	7	2	1								10	
1956-7	17	4									21	
1957-8	22										22	
Total 1949-58	82	36	4	2	0	0	0	0	0		124	54·6 ± 3·2
DENMARK, NORWAY AND SWEDEN												
Before 1949-50	31	13	6	6	0	0	0	0	0	0	56	
1949-50	0	1	1	1	0	0	0	0	0		3	
1950-1	1	3	0	0	0	0	0	0			4	
1951-2	9	3	1	0	0	0	0				13	
1952-3	3	1	1	0	2	0					7	
1953-4	7	4	1	2	0						14	
1954-5	4	2	2	2							10	
1955-6	17	8	4								29	
1956-7	19	15									34	
1957-8	9										9	
Total 1949-58	69	37	10	5	2	0	0	0	0		123	51·3 ± 3·5
POLAND, FINLAND AND U.S.S.R.												
Before 1949-50	25	9	5	1	1	0	0	0	0	0	41	
1949-50	0	0	1	0	0	0	0	0	0		1	
1950-1	2	0	0	0	0	0	0	0			2	
1951-2	2	1	1	0	0	0	0				4	
1952-3	1	1	0	1	1	0					4	
1953-4	1	3	8	0	0						12	
1954-5	2	8	7	0							17	
1955-6	10	18	2								30	
1956-7	25	3									28	
1957-8	5										5	
Total 1949-58	48	34	19	1	1	0	0	0	0		103	48·4 ± 3·8

life the average annual mortality-rate of the starling does not differ significantly from a constant rate of 55·5%.

Lack (1943, 1946) and Farner (1945) showed that in many passerine species, mortality in the first few months of life is greater than in subsequent years and that after the first January of life the annual mortality-rate becomes uniform. The starling was apparently an exception (Lack 1943) and the mortality in the first year (starting 1 August) was the same as in subsequent years. The data in Table 4 confirmed that mortality in the first year, starting at 1 August, does not differ from that in subsequent years. Having established this point, it is legitimate to use Haldane's method to obtain a more reliable estimate of the average

Table 4. *The mortality of nestling and juvenile starlings ringed before their first 1 August of life*

Birds ringed before 1950.

Year-group	Number dying	Number alive at beginning of year	Per cent dying during year	Number expected to die with a constant mortality-rate	χ^2
1	216	385	56·1	213·7	·02
2	92	169	54·4	95·1	·11
3	36	77		42·3	·93
4	29	41		18·8	5·53
5	6	12		8·4	·68
6	4	6	55·0		
7	0	2		6·7	·07
8	2	2			
over 8	0	0			
Total	385				7·34

Notes: 1. Mortality-rate from all year-groups is 55·5% per year.
2. Mortality-rate after first year = 54·7% which does not differ significantly from the mortality in the first year. ($\chi^2 = 0{\cdot}08$, 1 d.f. $P > 0{\cdot}8$.)
3. There is not a significant deviation from a constant mortality-rate irrespective of age ($\chi^2 = 7{\cdot}34$, 4 d.f.).

annual mortality. This had been used on two groups of starlings, first those which were ringed as juveniles before 1 August, and secondly those which were ringed as juveniles or first winter birds between 1 August and 31 December, inclusive, of their first year of life. Using data from birds which had been ringed before 1 January 1958, both methods gave an identical mortality of 54·4% per year (Table 5). It should be noted that the average annual mortality of birds ringed under 1 year old is greater than that of birds ringed of unknown age and presumably on average older, but the difference is not statistically significant.

SEASONAL CHANGE OF ADULT : JUVENILE RATIO

The percentage of starlings of known age recovered in each month of the year is shown in Table 6, along with the ratio of first-year birds to older birds. It is

Table 5. *Mortality of starlings ringed in Great Britain*

Birds ringed as nestlings or juveniles before 1 August

Year of ringing		Survival after the first 1 August of life (years)										Total	Average annual mortality (%)
		1	2	3	4	5	6	7	8	9	10		
Before	1950	140	62	22	19	5	3	0	2	0	0	253	
	1950	9	1	1	1	0	1	0	0			13	
	1951	4	3	3	1	2	0	0				13	
	1952	12	5	0	2	0	0					19	
	1953	3	2	1	0	0						6	
	1954	3	3	2	0							8	
	1955	6	2	0								8	
	1956	5	1									6	
	1957	0										0	
Total	1950-7	42	17	7	4	2	1	0	0			73	54·4 ±2·2

Birds ringed as juveniles and first-winter birds between 1 August and 1 January

		Survival after the first 1 January of life (years)										Total	Average annual mortality (%)
		1	2	3	4	5	6	7	8	9	10		
Before	1950	72	35	8	8	2	1	1	1	0	0	128	
	1950	16	8	1	2	3	0	0	0			30	
	1951	10	7	4	1	1	0	0				23	
	1952	27	6	8	1	0	1					43	
	1953	30	15	6	7	1						59	
	1954	34	16	9	3							62	
	1955	29	25	4								58	
	1956	48	7									55	
	1957	12										12	
Total	1950-7	206	84	32	14	5	1	0	0			342	54·4 ±2·1

Table 6. *Change in ratio of juvenile to adult starlings (recoveries)*

	Numbers recovered		Percentage juveniles
	Juveniles	Adults (>1 year old)	
July	41	5	
August	18	11	76
September	14	7	
October	14	8	
November	13	8	56
December	13	16	
January	23	10	
February	20	24	56
March	19	15	
April	33	21	
May	16	32	52
June	21	12	
July to December	47 (1 yr old)	35 (older)	57

evident that during July in particular, but possibly also in August and September, the proportion of young birds dying is greater than in subsequent months, a result which is a contradiction of the previous conclusion that the mortality in the first year is not different from the average. In the information in Table 6 the higher mortality during July, August and September is compensated by a lower mortality during the following breeding season. While this difference during the breeding season is not significant, it is sufficiently large to compensate for the larger mortality some 6 months earlier, making the mortality during the first year the same as in subsequent years. There may be some justification for expecting a lower

Table 7. *The mortality of adult starlings of unknown age at ringing*

Year of ringing		Survival after ringing (year-groups)										Total	Average annual mortality %
		1	2	3	4	5	6	7	8	9	10		
MALES													
Before	1950	79	47	17	8	6	5	1	0	0	0	163	
	1950	37	26	15	8	2	0	1	0			89	
	1951	40	32	20	9	4	3	1				109	
	1952	24	13	7	3	5	1					53	
	1953	23	14	5	3	1						46	
	1954	15	9	5	10							39	
	1955	37	23	12								72	
	1956	39	8									47	
	1957	14										14	
Total	1950-7	229	125	64	33	12	4	2	0			469	46·3 ± 1·6
FEMALES													
Before	1950	60	25	14	4	0	3	0	0	0	0	106	
	1950	36	26	7	7	3	0	0	0			79	
	1951	29	19	6	4	3	4	2				67	
	1952	25	7	9	5	2	3					51	
	1953	16	6	1	2	0						25	
	1954	22	10	7	3							42	
	1955	29	16	8								53	
	1956	35	8									43	
	1957	14										14	
Total	1950-7	206	92	38	21	8	7	2	0			374	49·9 ± 2·05

Note. A high proportion of the sexed starlings were ringed in the London area. This may account for the slightly lower mortality estimates of the sexed birds.

mortality amongst certain first-year starlings during the breeding season, since it is well established that a considerable proportion of the first-year birds do not breed (Kluijver 1935, Kessel 1957) and these may be exposed to less risk of mortality than the breeding birds. Of the recoveries of starlings where the cause of death is given, 22% are killed by cats during the first year as compared with 31% in subsequent years (the difference is not significant).

MORTALITY RATE OF MALE AND FEMALE STARLINGS RINGED AS ADULTS

Table 7 shows the distribution of recoveries, in years after ringing, of adult male and female starlings. The tables include all recoveries of birds ringed before 1958

and recovered before 1959. The male mortality is 46·3% per annum while that for the female is 49·9%; this difference (3·6±2·7%) is not significant, and it can be concluded that should a real difference exist between the mortality of male and female starlings, it is unlikely to be large.

THE SEX-RATIO IN THE STARLING

The sex-ratio of the starling has been determined from samples taken in both Europe and in the U.S.A., but little attempt has been made to study the sex-ratio of different age-groups systematically, although Kessel (1957) has added much new information. Table 8 summarizes the available information from literature on the sex-ratio of the starling and Table 9 gives additional information for

Table 8. *The sex-ratios of the starling in Europe and U.S.A.*

(*a*) Samples of the population including first-year birds

Country	Number of birds	Percentage males	Authority	
U.S.A.	2522	68	Hicks (1934)	Collected throughout the year
U.S.A.	473	65	Odum & Pitelka (1939)	Collected on 2 days
U.S.A.	285	45	Loefer & Patten (1941)	Collected in 1 week in March
U.S.A.	455	53	Stegeman (1954)	Collected on 1 day in March from a roost
U.S.A.	1359	58	Kessel (1957)	Collected December-March
Holland	305	52	Brouwer (1929)	
Holland	290	57	van Dobbin in Kluijver (1935)	85% of birds were adults.
Holland	813	69	Kluijver (1935)	Spring; trapped outside of breeding season
England	786	71	Bullough (1942)	Shot

Average percentage of males { in U.S.A. = 62 / in Europe = 66

(*b*) Sex-ratio of particular age-groups

U.S.A.	260	44	Kessel (1957)	Young 16-17 days old
England	101	63	Bullough (1942)	'Just off the nest'
U.S.A.	1168	52	Davis (1959)	First winter
U.S.A.	441	51	Kessel (1957)	First year
U.S.A.	746	58	Kessel (1957)	Adult
U.S.A.	715	66	Davis (1959)	Adult

Great Britain, derived from samples of starlings captured for ringing and aged and sexed by experienced ringers. These samples have been collected by different methods (shooting, trapping and collecting starlings from roosts) but they indicate that there was a preponderance of males in the population, in the ratio of about 1·8 males to each female. Kessel (1957) has shown that there are slightly more female starlings at the time of fledging (44% males), while during the first winter there are about 51% males. Again the data from first-year birds trapped in Great Britain (Table 9) indicated that 43% of the birds trapped were males. This supports Kessel's data that there is little or no differential mortality between the sexes from fledging to the first winter. Bullough (1942) recorded 63% males in a sample of 101 young starlings 'just off the nest', a value significantly different

from a 1 : 1 sex-ratio ($\chi^2 = 7{\cdot}2$ with 1 d.f. $P < {\cdot}01$). However, the sample taken by Bullough was small and apparently taken from a single locality on one day, and the validity of this as a typical sex-ratio could be doubted. Samples of first-year starlings trapped in Great Britain as late as March (and included in Table 9) still showed no preponderance of males, and it must be concluded that the differential mortality takes place some time after the first winter. Thus the sex-ratio shown in Table 8 (*a*) will underestimate the proportion of males in the adult population, since the first-year birds have a near equal sex-ratio. This difference is clearly shown in Table 9 where the total population of starlings has 60% males but the adult birds have 75% males. If the average adult sex-ratio is taken as 66% males (combining Davis's and Kessel's data with those in Table 9), it is possible to estimate the sex-ratio of the birds entering the adult population (adult plumage) from a life table derived from the mortality-rate of adult male and female starlings. This indicates that the sex-ratio is 62·5% males when the starlings enter the adult plumage. Thus it can be concluded that the differential mortality between male and female starlings takes place some time between the first March of life and attaining adult plumage in the next autumn. Further it is known that these birds have an average mortality of 56% in this year (Table 4) and

Table 9. *The sex-ratio of 1225 starlings captured for ringing in Great Britain, 1950-57*

	Adult		First-year		Total	
	Males	Females	Males	Females	Males	Females
Number	505	169	235	316	740	485
Percentage males	75		43		60	

that the sex-ratio changes from about 46% males (pooled British data) to 62·5% males. There is only one possible explanation for this situation; the males, which comprise 46% of the population, must have a mortality of 39% while the female mortality is 70% for the year. These mortality-rates give an average mortality of 56% for the year and change the sex-ratio to 62·6% males.

Further evidence of a differential mortality between male and female starlings before they attain an adult plumage is given in Table 10. While the differences between the proportion of males and females recovered between January and July (when they are about 1 year old) is not significant, a difference is present, and the results are compatible with the mortality-rates shown above, if allowance is made for additional recoveries of old birds which are still alive.

ADULT MORTALITY

(*a*) *Average annual adult mortality according to region*

The recoveries of birds of unknown age (but more than 6 months old) were analysed according to the region in which the birds were recovered and, in the great majority of cases, this was also the region of ringing. The following five areas were chosen:

(1) *Northern Region:* Consisted of the Scottish mainland and Cumberland, Westmorland, Northumberland and Co. Durham.

(2) *Central Region:* Including Yorkshire, Lancashire, Cheshire, Lincolnshire, Nottinghamshire, Derbyshire, Staffordshire, Shropshire and North Wales (bordered by the southern border of Montgomeryshire).

Table 10. *Recoveries of male and female starlings in the seven months, January-July of their first year*

	Number dying January-July	Number dying more than 1 year old	Total
Females	37 (52%)	34 (48%)	71
Males	24 (37%)	41 (63%)	65

Notes (i) Use has been made of all recoveries up to and including 1958.
(ii) Some birds belonging to the second column are probably still alive and remain to be recovered.

(3) *London Region:* A relatively small, highly populated area, defined as the area within a radius of 17 miles of Westminster Bridge.

(4) *South-east Region:* This region excludes the London region and contains Cambridgeshire, Northamptonshire, Rutland, Leicestershire, Buckinghamshire, Middlesex, Surrey, Sussex, Norfolk, Suffolk, Essex, Kent, Lincolnshire and Hertfordshire.

Table 11. *Average annual adult mortality of the starling in different regions of Great Britain*

Birds ringed before 1950

	Survival after ringing (year-groups)										Total	Average annual mortality (%)
	1	2	3	4	5	6	7	8	9	10		
North	91	55	30	14	8	1	1	0	1	0	201	49·2 ± 2·5
Central	208	107	43	26	5	5	4	0	0	0	398	53·9 ± 1·75
South-east	104	64	27	11	3	2	1	1	0	1	214	52·3 ± 2·5
South-west	182	86	39	21	13	8	1	1	0	0	351	51·4 ± 2·0
London	73	43	20	13	2	4	2	0	0	0	157	49·2 ± 2·8
Total	658	355	159	85	31	20	9	2	1	1	1321	51·6 ± 1·01

(5) *South-west Region:* Includes south Wales (south of the southern border of Montgomeryshire), Herefordshire, Warwickshire, Worcestershire, Oxfordshire, Berkshire, Hampshire, Devon, Cornwall, Somerset, Gloucestershire, Dorset and Wiltshire.

The recoveries of starlings ringed before 1950 were used and the results are shown in Table 11. No significant differences were observed between the five groups but the lowest mortality-rates were recorded in the Northern and London Regions.

Too few starlings have been ringed in Ireland to give a reliable estimate of their mortality. Unfortunately it has not been possible to analyse the mortality according to urban, suburban and rural areas, but the different mortality-rate of starlings which were shot, suggests that differences might occur.

(*b*) *Monthly variation in recoveries of adult starlings*

From a study of the ringing recoveries of American ringed starlings, Kessel (1957) showed that the majority of recoveries occurred in January, February and March, but in Great Britain the recoveries reached a peak during April and May (Fig. 3), although the breeding season in both areas is almost the same. The difference is even more striking when it is remembered that the resident population in Great Britain is supplemented between October and March by wintering Continental starlings and recoveries of these birds would tend to increase the numbers recovered in these months. Neither of the distributions in Fig. 3 may represent the true seasonal distribution of mortality. During the winter and the

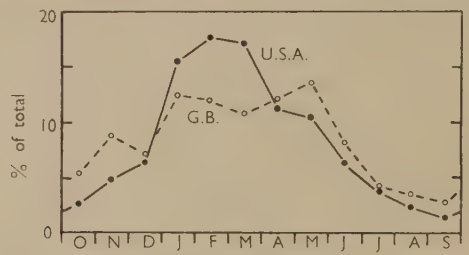

Fig. 3. A comparison of the monthly recovery rate of starlings ringed in the United States and Great Britain.

breeding season many starlings spend much time close to human habitation, while the majority appear to move out during the summer into the country, well away from human habitation. According to Kessel (1957) the starling in America behaves in a similar manner. It would be expected that a greater proportion of dead starlings would be recovered during the time of year when they are feeding or breeding near habitation. Likewise, it might be expected that a dead bird would not decompose as rapidly during the winter months and, owing to the reduced amount of vegetation, be more likely to be recovered. Alternatively, the shorter day length and a tendency for man to remain indoors during the winter, would tend to reduce the chances of recovery. However, comparative differences, like those in Fig. 3, are likely to be real.

(*c*) *Annual variation in adult mortality of the starling*

Table 12 gives the numbers of adult starlings which were recovered according to the year of ringing and the year of recovery. From this 'trellis' diagram, it is possible to estimate the mortality in each individual year (Fig. 4). For instance, in the part of the table enclosed by a black line, those in the column at the left

side of the rectangle died during the year 1934-5 while the total number of recoveries in the rectangle gives an equivalent measure of the number of starlings which were at risk during that year. Thus the annual mortality can be determined from these two numbers; *i.e.* 71 died out of a possible 155 which gives a mortality of 45·8%. The annual mortality was estimated for the year beginning on 1 April so that the possible effects of the winter climatic conditions could be related to the mortality; this date was also an advantage because most birds were ringed during the winter, and this made the most use of the available information. The extreme mortality-rates from years in which more than 100 birds were at risk (12 years)

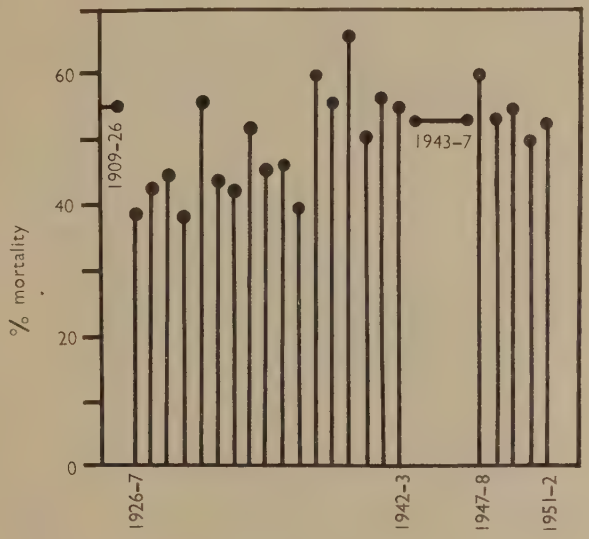

Fig. 4. Annual variation in the mortality rate of the starling.

are 66% in 1939-40 and 40% in 1936-7 and the annual variations are shown in Fig. 4.

(*d*) *Annual adult mortality and climate*

The annual mortality was grouped according to the severity of the winters concerned. The number of nights with frost, the number of days with snowfall and the number of days with snow lying were determined from five stations (Aberdeen, Cranwell, Ross-on-Wye, Tynemouth and Kew Gardens) and averaged for each year from 1926-7 to 1951-2 and the results are presented in Table 13 together with the mortality. There was only a small increase in the annual mortality with an increased severity of the winter weather.

(*e*) *Bimonthly and regional variation in causes of adult mortality*

The bimonthly variation of recoveries according to the cause of death is shown

Table 12. *The recoveries of starlings according to the year of ringing and the year of recovery*

Each year runs from 1 April to 31 March in the following calendar year. The box shows how the individual annual mortalities were calculated, the sum of all the figures in the box giving the number of birds at risk, while the left-hand column shows the number which died in 1934–35

| YEAR OF RINGING | YEAR OF RECOVERY | | |

in Fig. 5. The causes of death show a tendency to form a peak during the breeding season with the exception of shooting and flying into telephone

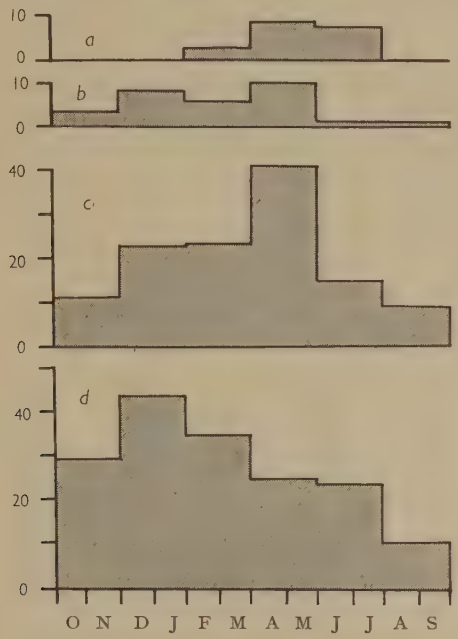

Fig. 5. The bi-monthly variation of certain reported causes of death of the starling: *a*, drowned; *b*, falling down chimney; *c*, killed by cats; *d*, shot. Note the winter peak of deaths caused by starlings being shot, while there is a peak of deaths caused by cats during the breeding season.

wires. The number of starlings killed by cats shows a distinct peak during the breeding season, 33% of recoveries of starlings due to cats occurs in the 2 months of April and May, while only 16% of the total shot, occurred during

Table 13. *The effect of winter weather on the mortality of the starling*

		Number of years	Number of birds		Percentage dying
			Alive	Died	
FROST					
Number of days on which ground frost was recorded	<60	10	1192	602	50·2 ± 1·4
	60–69	6	566	288	50·9 ± 2·1
	>69	6	1393	750	53·8 ± 1·3
SNOW					
Number of days on which snow fell in the year	<20	12	1390	716	51·5 ± 1·3
	20 or more	10	1761	924	52·5 ± 1·2
Number of days with snow lying	0–6	12	1280	640	50·0 ± 1·4
	>6	10	1871	1000	53·4 ± 1·15

this time. Fig. 6 shows the different proportions of starlings which were recorded as shot or killed by cats in the five regions of Great Britain (see p. 263). In the

south-east and south-west regions, there was a high proportion of shot birds while in the London region very few starlings were shot, but there was a corresponding increase in the proportion killed by cats.

DISCUSSION

There is little literature which deals with the seasonal mortality of the starling, and such data are difficult to obtain owing to many variables which affect finding of dead birds. Dunnet (1956) has suggested that there might be a high mortality of starlings in the autumn and winter, but his argument is based on theoretical considerations and he does not support his statement with observations. Likewise his statement that mortality in birds is low during the breeding season is not supported. There are reports of starlings dying during severe winters (*e.g.* Ticehurst & Hartley 1948), but the extent of this mortality is difficult to determine

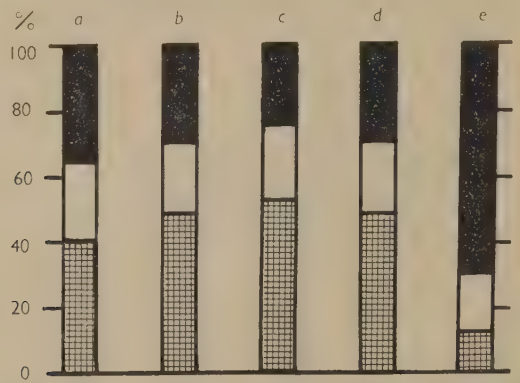

Fig. 6. Regional variation in the cause of recoveries of starlings. Only recoveries have been used where a cause of death has been reported. The white part of each histogram represents miscellaneous causes of mortality such as drowning, falling down chimneys and flying into telephone wires, the black portions cats, and the hatched portion shooting. The regions are: *a*, North; *b*, Central; *c*, South-west; *d*, South-east; *e*, London.

quantitatively by means of questionnaires. Hicks (1934) has studied the weight and distribution of the fat layer on starlings in Ohio, U.S.A., and concluded that this layer was not lost until 4 or 5 days after the onset of very severe weather. Dunnet (1956) has come to a similar conclusion from observations in Great Britain and showed that there was relatively little loss in the fat layer during a prolonged snow-cover, apparently because the starlings were obtaining food around habitation. It is probable that only long periods of cold weather with the temperature well below freezing point and particularly deep snow lasting for more than 4 days are capable of producing extensive mortality by starvation. In Great Britain, such severe climatic conditions are relatively rare, while wide-spread and complete snow-cover lasting more than 4 days is uncommon. The present investigation has shown that there is only a very poor relationship between the severity of the winter and the mortality-rate of the starling. This suggests that the winter

weather in Great Britain is rarely sufficiently severe to increase the annual mortality appreciably.

The percentage of males amongst first-year starlings apparently increases by about 17% during the period from the first March of life to the following August (*i.e.* in the year following hatching). This change is produced by a marked difference in the mortality-rates of first-year male and female starlings, the mortality of the females being almost twice that of the males. This difference in mortality-rates takes place over a relatively short time and strongly suggests that there must be a marked difference between the behaviour of the sexes during this period. The most obvious difference is that the majority of the first-year females are capable of and succeed in breeding, while few males are physiologically capable of breeding (Kluijver 1935, Bullough 1942, Kessel 1957). This implies that there is probably an increased risk associated with breeding, at least amongst young birds. Female starlings spend more time incubating and collect more food for the young than do the males (Kluijver 1933) so it is probable that there is not such a marked increase in mortality of males breeding for the first time. This mortality during the breeding season is likely to be caused by predation, since it has to operate selectively on the female starlings. The most likely predator, particularly during the breeding season, is the domestic cat. Fig. 5 shows the marked increase in the number of recoveries of adult starlings killed by cats during the breeding season. It has been shown that nestling starlings require almost their own weight in food each day (Kluijver 1935) and the effort involved in collecting this amount of food for a brood of four or five young must cause the parents to spend a much greater time on the ground searching for food. This, in turn, is likely to make the breeding birds more liable to capture by cats.

Little information is available upon the numbers of domestic cats in relation to habitation, but Matheson (1944) reports that 26-76% (depending upon the district) of households in Cardiff and Newport had cats, and estimated that there were about 13 cats for every 100 people in these towns. In rural areas it would seem likely that these figures would be even higher, since most farms have at least one cat. More recently, it has been estimated that there are 500 000 cats in the County of London, and this is equivalent to about five cats to every starling in this area (Fitter 1949). Since many starlings breed in close proximity to human habitation (Davies 1949) it is clear that the number of cats are sufficient for them to be an important predator of the starling.

ACKNOWLEDGMENTS

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The present investigation was carried out while the author was holding a Senior Studentship awarded by the Royal Commissioners for the Exhibition of 1851.

SUMMARY

1. The mortality-rate of the starling (*Sturnus vulgaris*) has been studied by using some 7000 recoveries of ringed individuals.

2. Estimates of the average annual adult mortality differ with the cause of recovery. The recovery of starlings which had been shot gave a mortality-rate some 9% greater than that determined from other causes. It is suggested that this difference reflects a higher mortality-rate in areas where starlings are shot rather than that young birds are more liable to be shot.

3. The mortality-rate of the starling in Great Britain is estimated as $52{\cdot}8 \pm 1{\cdot}0\%$. This value does not differ significantly in different regions of Great Britain, nor for foreign starlings which have wintered in Great Britain.

4. The annual mortality-rate of the starling does not change after the first 1 August of life, but first-year birds experience a greater mortality in their first autumn and winter, which is compensated by a probable lower mortality during the following spring.

5. The sex-ratio of the starling changes over a short period at the end of the birds' first year to give a marked predominance of males. This can only be explained by a male mortality of 39% and a female mortality of 70% in the first year of life from 1 August. This differential mortality probably arises through more first-year females than males breeding in their first year.

6. The number of recoveries reaches a peak during the breeding season, mainly owing to the capture of starlings by cats. It is likely that the act of breeding increases the risk of death to starlings since they need to spend more time on the ground collecting food for their young.

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MIDNIGHT-SUN ILLUMINATION ABOVE AND BELOW THE SEA SURFACE IN THE SÖRGAT, N.W. SPITSBERGEN, AND ITS SIGNIFICANCE TO PLANKTON

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(With 9 Figures in the Text)

The diurnal and seasonal changes in illumination below the sea surface in low latitudes have a considerable influence on vertical distribution of marine plankton organisms. The subject has been reviewed by Russell (1927) and by Cushing (1951). Many plankton animals are found close to the surface at night and at greater depths during the day, and the observations of Clarke (1933) on *Metridia* and of Russell (1934) on *Calanus* and other organisms have shown that they tend to congregate in a zone of preferred light intensity, and so far as possible to follow this zone as it changes position through the twenty-four hours.

During the arctic summer the sun remains above the horizon and the changes of illumination are more limited. Comparatively little is known of the extent to which these smaller changes may influence the vertical position of the plankton. Some early observations, for instance those of Walter (quoted by Walther 1893) on medusae and Römer (1904) on ctenophores (quoted by Russell 1927) suggested that substantial vertical movements might still occur under midnight-sun conditions. On the other hand Bogorov (1938, 1941, 1946) found that populations of copepods showed no diurnal migrations in the Barents and White Seas under summer midnight-sun conditions, although such movements did occur during autumn.

No actual measurements of the diurnal changes of illumination below the sea surface have been made under these conditions, and although Russell (1927) estimated that these changes were probably not inconsiderable, the effects of cloud cover and transparency are uncertain.

Measurements and collections were therefore made in Spitsbergen in 1956 to obtain further information both on the extent of the changes of light intensity and on the distribution and movements of the plankton. This paper describes the observations of illumination and transparency, and the estimation of light intensity below the sea surface. Few observations of illumination as such have been made in these regions; in Spitsbergen Lindholm (1938) carried out a series of measurements with a grey-wedge photometer; these measurements cannot readily be compared with those obtained from other instruments. Illumination may, however, be obtained from solar radiation, measurements of which are often made as it is a quantity of meterological importance. Series of radiation measurements in Spitsbergen have been described by Westman (1903), Götz (1931), Ångström (1933) and Olsson (1936 a, b). Those made on the Siberian Shelf by the *MAUD*

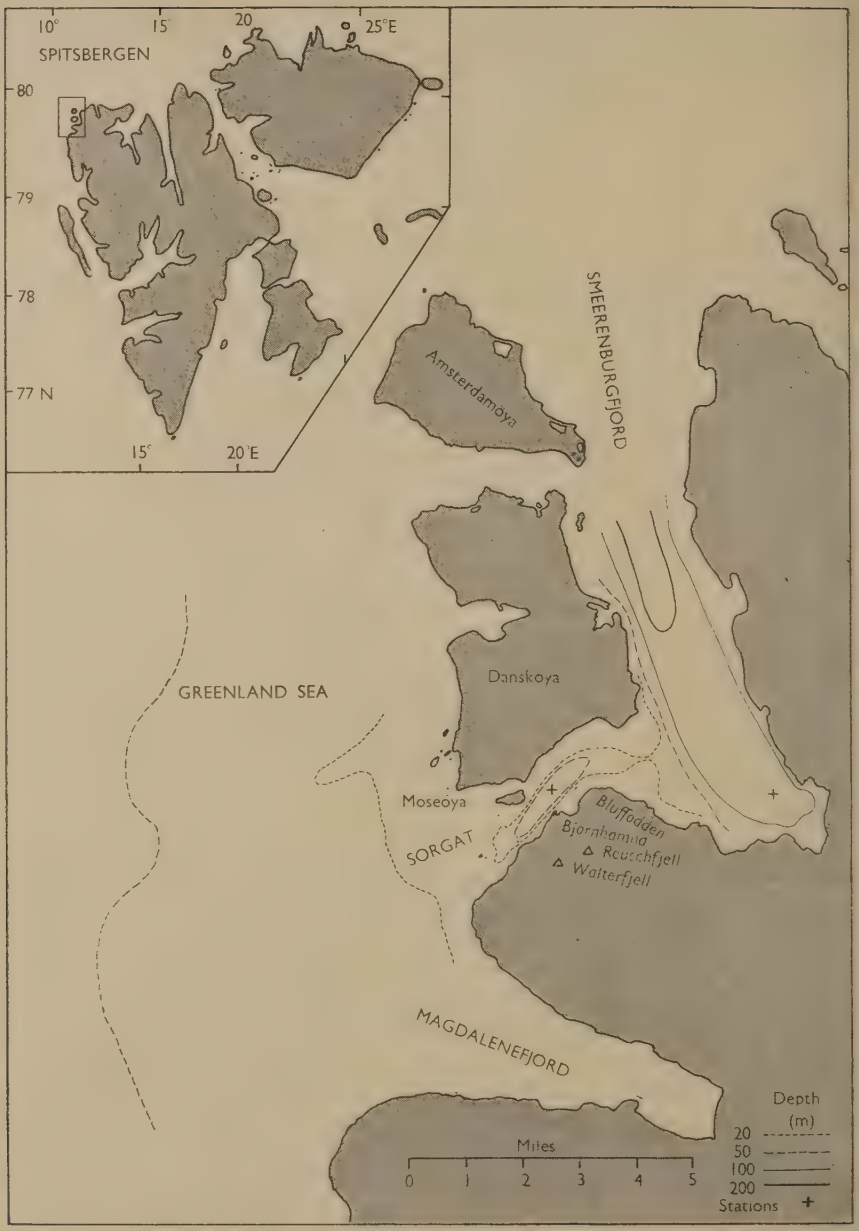

Fig. 1. Sketch map of Spitsbergen showing positions of stations.

expedition (Mosby 1932) are probably also characteristic of this region. The only transparency measurements made in these waters appear to be a series of Secchi disc observations by Mosby (1932).

The work was greatly facilitated by the kindness of the Norwegian authorities who made it possible to carry it out during July and August at the hut at Bjornhamna on the south side of the Sörgat, which is the channel leading from Smeerenburgfjord to the open Greenland Sea separating Danskoya from the mainland in 79° 39′ N, 10° 59′ E. (Fig. 1).

METHODS

A record of illumination in air was obtained from a photocell and recording

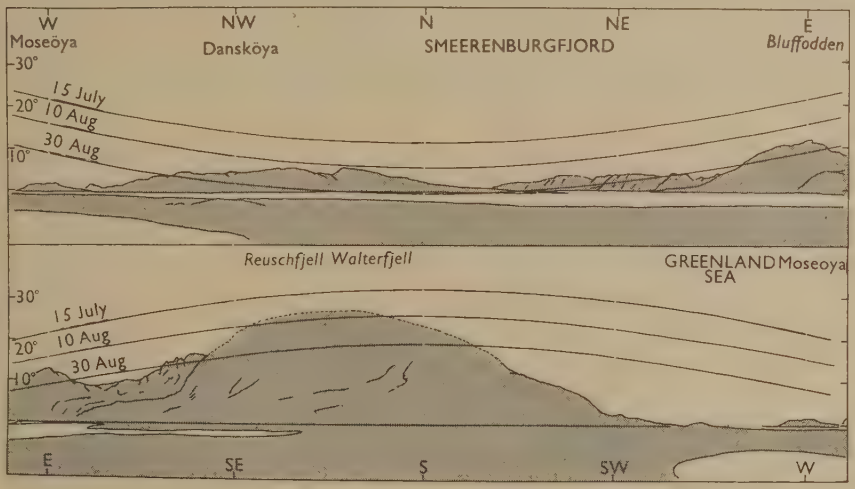

Fig. 2. Panorama from the hut at Bjornhamna in the Sörgat where the illumination measurements were made, with superimposed tracks of the sun.

meter at the hut at Bjornhamna, while light intensity below the surface was calculated from values above the surface together with the transparency, by methods similar to those used by Poole & Atkins (1926, 1929), Atkins & Poole (1933) and Clarke (1933). These methods were reviewed by Atkins, Clarke, Pettersson, Poole, Utterback & Ångström (1934).

The photocell measuring the vertical component of light intensity above the surface was mounted on the roof of the hut. Light measurements were obtained from 15 July to 25 August; over this period the solar altitude declined from 31° 54′ to 21° 01′ at noon and from 11° 14′ to 00° 21′ at midnight. These values are derived from the *Nautical Almanac* and exclude refraction which causes the sun to appear 30′ higher than its true position when close to the horizon. By 15

July, when these observations were begun, the solar altitude at noon and midnight had declined roughly 2° from their highest value on 21 June. The calculated paths of the sun throughout the 24 hours on 15 July, 10 August and 30 August have been superimposed on a panorama obtained from a complete round of photographs taken at the hut (Fig. 2). The path of the sun was at first unobscured by the contours of the land, but after 10 August it passed behind mountains both to the south and to the north; the northern part of the sun's track was the less obscured.

Transparency measurements and plankton collections were made a short distance away in the centre of the Sörgat. A 17-ft Norwegian rowboat used with an outboard motor and fitted with a winch and metre wheel inboard was used for this purpose, as previously in Greenland (Digby 1953). Temperature measurements were made with a Pettersson-Nansen insulating waterbottle, samples for salinity being brought back and titrated in England by the Government chemist. Net phytoplankton pigment assessments were made on plankton hauls made with an Apstein net suitably modified as before by fitting a water meter.

HYDROGRAPHY AND PHYTOPLANKTON

The relatively warm current which runs to the north-east round the northern part of Spitsbergen, the Spitsbergen Atlantic Current (Mosby 1938) results in this part of the coast being comparatively free of ice. In July and August the edge of the Polar ice commonly lies 50 or more miles to the north. The tides are fairly strong in the Sörgat and the current passes over a shallow area of 10-20 m depth at the eastern and western ends, which results in some turbulence. Measurements of temperature and salinity (Table 1) showed the water column at Sörgat to be very weakly stratified, temperatures ranging from 4·77 to 6·17 C with a maximum at 1 m on 3 August. Salinities ranged from 32·95 to 34·62‰ with a minimum at 1 m on 1 August. The single series in Smeerenburgfjord, 2 miles from the snout of the Smeerenburg glacier, was very similar to those in the Sörgat. In some places in Spitsbergen, close to the mouth of the rivers and to the ends of the large glaciers in the fjords, the turbid fresh water from the melting snow and ice spreads over the surface of the fjords as thin sheets, moved about by wind and tide. In the Sörgat these drifting sheets of turbid water were not encountered; the sea here receives a comparatively small amount of freshwater run-off.

Phytoplankton may at times be very dense in arctic waters. By the time these observations in the Sörgat were made, however, the main period of phytoplankton production was over. Pigment densities assessed from the catch of a metered Apstein net (Digby 1953) were very slight (Table 2), they ranged from 5·0 to 51 Harvey units m^3, while occasional membrane pigment samples, as at Scoresby Sound (Digby 1953) gave no indication of any substantial bulk of pigmented net-passing organisms. The fine net material consisted mainly of large numbers of nauplii and tintinnids with a few dinoflagellates, representing a late stage of the phytoplankton cycle.

CLOUD

The cloud cover at Sörgat, recorded in tenths every 3 hours so far as possible, and the occurrence of strong or weak sunshine, is shown in Table 3. These observations were made at approximately European mean time, 1 h in advance of GMT and roughly 20 min in advance of local apparent time (LAT; the time as would be indicated by a sundial and at which illumination readings were subsequently

Table 1. *Temperature and salinity*

TEMPERATURE (° C)	Depth (m)							
	1	5	10	20	30	50	70	100
19 July	4·77		4·69		4·64			
21 ,,	4·82	4·76	4·77	4·72	4·73	4·77		
25 ,,	4·95		4·95		4·95			
27 ,,	5·22		5·22		5·22			
30 ,,	5·16		5·05		5·02			
1 August	6·12		6·05		5·31			
3 ,,	6·17	6·00	5·69	5·64	5·45	5·22		
7 ,,	*5·43		5·55	5·00	4·37	4·25	3·85	2·05
12 ,,	5·14		5·13		5·13			
13 ,,	5·44							
13 ,,	5·35							
14 ,,	5·22							
14 ,,	5·04							
15 ,,	5·17							
15 ,,	5·24							
21 ,,	5·64		5·47		5·22			
21 ,,	4·99							
22 ,,	5·35							
22 ,,	5·17							
23 ,,	4·77							
24 ,,	4·95							
24 ,,	4·99							
25 ,,	5·19		5·14		5·11	5·10		
SALINITY (‰)								
21 July	34·05	34·13	34·11	34·26	34·19	34·13		
27 ,,	34·05		34·01		33·99			
30 ,,	33·87		34·07		34·02			
1 August	32·95		33·53		33·92			
3 ,,	33·29	33·38	33·55	33·70	33·91	34·02		
7 ,,	*33·22		33·62	34·00	34·57	34·58	34·54	34·62
12 ,,	34·00		33·94		33·98			
21 ,,	33·35		33·52		33·78			
25 ,,	33·63		33·64		33·68	33·73		

* Station in Smeerenburgfjord.

taken from the recorder). Although these observations did not cover the whole 24-hour period each day, they are sufficient to show that overcast conditions prevailed most of the time, periods of a day or so of sunny weather occurring at intervals of 5-7 days. Monotonously overcast weather with thin sheets of stratus is the rule for the maritime arctic seas in summer (Sverdrup 1933) and this locality is no exception. Numerous observations of cloud cover have been made in Spitsbergen; that at 'Sveanor' (Murchison Bay, at the northern end of the

Hinlopen Strait) in the summer of 1931 was very similar, and it, and the climatology of this region during that time has been described by Ericksson (1933).

ILLUMINATION ABOVE THE SEA SURFACE

(*a*) *Recording apparatus*

Light intensity was recorded by a 4·5 cm diameter barrier-layer cell (Evans Electroselenium Co. Ltd.) shunted by a 170 ω resistance and connected in series with a further 170 ω resistance to a pen recorder (Record Electrical Co. Ltd) of 140 ω resistance and 1 mA full scale deflexion. The photocell, covered by a

Table 2. *Phytoplankton and Secchi-disc observations*

	Net phytoplankton pigment (Harvey units/m³)	Membrane pigment samples	Secchi-disc reading (m) r = comparative value with Secchi-disc seen against sky reflection
15 July			7·5
17 „	<10		
19 „	<10		6·0
21 „	<6·5	+	6·25
25 „	5·0		6·0
27 „	<21·0	+	6·5, 7·5 (r 4·0 with strong diffuse glare)
30 „	13·5	+	7·0, 7·4
1 August	<10·5		6·75 (r 5·5)
3 „	<6·0	+	6·1
7 „	19·0	+	4·25, 3·0, 3·75
12 „	51·0	+	6·0, 8·25, 8·75
12 „			8·75, 8·8
13 „			7·6 (r 7·5), 8·2
13 „			8·5 (r 7·8), 8·8 (r 8·0)
14 „			8·25, 8·9 (r 8·5)
14 „			8·5, 8·0
15 „			6·25, 7·0 (r 6·5)
15 „			7·4, 8·25
21 „	10·2	+	8·75
21 „			10·0, 9·4
22 „			9·5, 9·25
22 „			10·9, 9·3
23 „			8·75, 9·2
24 „			9·0, 9·5
24 „			7·25, 7·8
25 „	<7·5		9·5

single thickness of wire gauze to serve as a neutral filter, was mounted in a waterproof housing, the window of which was covered by a flashed opal, opal side uppermost. Incident light was reduced to about one-tenth by the opal and gauze before falling on the cell, and with the circuit amounting to an external resistance of 163 ω across the cell, the relation between the meter deflexion and light intensity was linear up to 15 klx and curved above this value. The circuit rendered the influence of changes of temperature on the meter readings almost negligible. The meter deflexion could be read to $\pm 10\%$ at the lowest light intensity encountered (0·5 klx) and to $\pm 0{\cdot}5\%$ in the upper part of the scale.

The recorder was calibrated by comparison with a standard consisting of a 3·5 cm diameter barrier-layer cell covered by a flashed opal and a neutral filter, connected to a Cambridge 'Unipivot' galvanometer, Type LX (internal resistance

Table 3. *Cloud cover and sunshine*

Cloud in tenths; italic figures, weak or occasional sunshine; bold figures, strong sunshine

	Time								
	0000	0300	0600	0900	1200	1500	1800	2100	2400
15 July	–	–	–	–	**<1**	**<1**	–	9	9
16 „	9	10	–	–	10	10	10	10	10
17 „	10	–	–	–	10	10	10	10	10
18 „	10	–	–	–	10	7	*7*	**6**	10
19 „	10	–	–	–	10	*7*	10	10	–
20 „	–	–	10	10	10	10	10	10	10
21 „	10	–	–	10	10	–	9	10	9
22 „	9	–	–	**1**	*9*	10	10	10	–
23 „	–	–	–	**3**	**2**	**2**	**3-9**	**3-9**	10
24 „	10	–	–	–	10	10	10	10	10
25 „	10	–	–	10	10	10	10	3–9	**3**
26 „	**3**	–	–	*8*	10	10	10	10	*9*
27 „	*9*	–	–	**5**	*10*	8	8	8	5
28 „	**5**	–	–	**1**	**1**	**1**	*5*	*10*	10
29 „	10	–	–	–	**<1**	**<1**	**<1**	**<1**	**<1**
30 „	**<1**	–	–	–	9	9	*8*	**8**	**7**
31 „	**7**	–	–	–	10	10	10	10	10
1 August	10	–	–	–	10	10	10	10	10
2 „	10	7	–	–	*10*	10	10	10	9
3 „	9	–	–	**1**	6	10	10	10	10
4 „	10	–	–	–	10	10	10	10	10
5 „	10	10	–	–	10	9	9	9	9
6 „	9	10	–	–	10	10	10	10	10
7 „	10	10	–	–	10	10	10	10	10
8 „	10	–	–	–	**4**	**1**	**3**	**6**	**4**
9 „	**4**	–	–	–	10	10	10	10	*9*
10 „	*9*	–	–	–	8	9	10	10	10
11 „	10	–	–	–	10	10	10	9	10
12 „	10	–	–	–	10	**2**	**1**	*3*	10
13 „	10	–	–	–	10	10	10	10	10
14 „	10	10	10	–	–	10	10	10	10
15 „	10	–	10	10	10	10	10	10	–
16 „	–	–	–	–	10	10	10	10	10
17 „	10	10	–	–	10	10	10	9	10
18 „	10	–	**3**	**2**	**1**	**1**	**1**	**5**	10
19 „	10	–	–	–	10	10	10	10	10
20 „	10	–	–	–	10	10	10	10	10
21 „	10	–	–	10	10	10	9	8	*2*
22 „	*2*	–	–	**0**	**3**	**8**	**8**	**7**	**3**
23 „	**3**	–	–	–	*8*	10	10	10	8
24 „	8	5	5	*9*	–	9	*9*	*6*	*1*
25 „	*1*	–	–	–	10	10	10	10	10
26 „	10	–	–	–	10	10	10	10	10

10 ω, full-scale deflexion 0·1 mA). The cell, opal and galvanometer were previously calibrated in the laboratory against a 1000 W standard tungsten filament lamp at 2854° K standardized at the National Physical Laboratory the previous year. Calibration curves were made out for the cell with the opal alone and with

one or the other of two neutral filters inserted between the cell and the opal. Two additional calibrated cells were used as a check on the stability of the first cell. This field standard was used to calibrate the recording cell and meter when set up and running.

(*b*) *Corrections*

It was necessary to consider certain corrections to the calibration reading to account for spectral sensitivity, angle of incidence of the light and occlusion of the sky.

Since the barrier-layer cell differs in spectral sensitivity from the human eye, a correction factor is needed if it is used to measure light of a different spectral composition to that with which it is calibrated. A correction could have been obviated by the use of a suitable green filter; Atkins & Poole (1936a) used a green gelatine filter; a three component glass filter is in use at Kew (G. E. Robinson, personal communication; Blackwell 1953). As only a single suitable light green filter was available at the time these measurements were made and it was desired to use this in the transparency apparatus, the cell attached to the recorder was used without a correcting filter and a correction factor was calculated. Atkins & Poole (1936a) found a Weston selenium cell to be 1·15 times as sensitive to 2360° K radiation as to artificial mean noon sunlight prepared by using a lamp behind a Davis-Gibson filter and applying the accepted figure to the percentage transmission of the filter. This would give a correction factor of 0·87. In the present work a factor of 0·82 was used; this was arrived at by calculation from the relative sensitivity of the photocell and of the human eye to the tungsten lamp at approximately 2850° K and to 'average daylight' of 6500° K (Judd 1933), considered at intervals of wavelength of 20 Å. The spectral sensitivity of the photocell was taken from the maker's published curve, that of the human eye from the data of Judd (1933).

Light at a low angle suffers almost total Fresnel reflection at the polished surface of the opal glass window covering the cell. A correction must therefore be applied after calibration in light of normal incidence. Largely owing to uncertainties attached to this correction, light measurements with a photometer of this type are intrinsically of lower accuracy than are measurements of radiation which is measured by absorption on a blackened surface not exhibiting such reflection. This correction was calculated by methods similar to those of Poole & Atkins (1926), but with certain differences. Poole & Atkins obtained their correction by calculating the proportion of total sky-light falling on the horizontal window from the area of sky enclosed within successive increments of altitude, regarding the sky as uniformly lit, and applying to each the appropriate correction for calculated Fresnel reflection from a plain glass surface. In the present case the overcast sky has been assumed to be brighter at the zenith than at the horizon and the characteristics of opal glass have been used instead of those of clear glass for the transmission of the photometer window. The sky at Sörgat was overcast during most of these observations, and with an overcast sky and non-reflecting ground

surface in Britain the zenith is three times as bright as the horizon (Moon & Spencer 1942). This depends on lack of reflection of light from the ground; at Sörgat the reflectivity of the surrounding land surface was probably small, because although there are extensive snow fields and glaciers inland, there is a great deal of darkly coloured rock exposed in this region at this time of the year, and the sea surface has a reflectivity of only 0·051 for diffuse light when smooth (Middleton 1952) and probably little more when the surface is broken. Middleton's expression relating brightness to altitude has therefore been assumed to hold good for Sörgat. The fraction of incident light which penetrates the opal has been obtained by multiplying the proportion of total sky-light incident on its surface from each interval of 10° altitude by the brightness of opal glass for light at the corresponding angle of incidence. The figures for the latter were taken from the diagram given by Walsh & Buckley (1929) for the relation between brightness of opal glass and the angle of incidence of light; they agree essentially with those found by Blackwell in correcting the readings of the Kew photometer (Blackwell 1953) and differ considerably from those arising from simple Fresnel reflection. This procedure yields a correction factor of 1·09, which has been used in this paper. If the sky were assumed to be uniformly bright, the factor would be 1·12. These factors may be compared with that of 1·06 used by Poole & Atkins (1926, 1935) and Atkins & Poole (1936b) in correcting their photometers for the reflection losses in diffuse light. In this paper the two correction factors of 0·82 for spectral response and 1·09 for reflection of diffuse light have been applied together to all photometer readings by multiplying the values read from the calibration curve by 0·985.

When the correction for diffuse light is applied to all measurements the illumination with sunshine is underestimated because of reflection of the direct rays of the sun from the surface of the opal when the sun is at a low altitude. In order to correct fully for this it is necessary to know the respective amounts of direct and diffuse light, and to correct for each separately (Poole & Atkins 1926). No measurements of these proportions were made at Sörgat, and there appear to be no suitable values of diffuse illumination available for the Arctic. The proportion of direct to total solar radiation under cloudless conditions in these latitudes have, however, been given by Mosby (1932) in his account of the radiation measurements made during the drift of the *MAUD* off the northern coast of Siberia. Mosby's figures are very similar to those obtained by Kimball (1924) for the U.S.A., and it is probable that conditions in Spitsbergen are the same. A selection of Mosby's values for the proportion of direct to total radiation are as follows:

Altitude of the sun	3°	5°	10°	20°	30°	40°
Proportion, direct/total solar radiation	0·4	0·5	0·65	0·75	0·79	0·81

The luminous efficiency of sky-light was shown by Atkins & Poole (1936a) to be roughly twice that of direct sunlight as recorded by a selenium cell, and by applying this to Mosby's figures we may obtain an estimate of the correction factor to apply to photometer readings made in sunshine with little or no cloud (that is,

the factor to apply in place of the 1·09 used to correct for diffuse light). This factor is:

Altitude of sun	3°	5°	10°	20°	30°
Correction factor	1·6	1·44	1·36	1·17	1·15

This correction for the reflection of direct sunlight from the opal is insignificant compared with the change in illumination arising from change of solar altitude. It becomes of importance, however, in considering the attenuation of light by cloud cover.

A possible need for correction arises from occlusion of part of the sky by surrounding hills. Measurements from a complete round of photographs taken close to the recorder showed that roughly 67% of the sky between 0° and 10° altitude, 25% between 10° and 20°, and 7·8% between 20° and 30° was occluded (Fig. 2). The light from this part of the sky is at a low angle and much would normally be reflected at the surface of the opal. Taking this into account and assuming as before that overcast conditions prevail with the zenith three times brighter than the horizon, the correction applicable would be a maximum of 1·07 if all the visible land were totally non-reflecting. As some of the horizon during the period of observation consisted of snow-covered ground this maximum would not usually be reached and 1·05 would be a more appropriate correction factor. This would, however, be exceeded when, as occurred on a few occasions in August, bright sunshine prevailed and a direct shadow of the mountain behind the hut fell across the recorder for a short period during the morning. Under conditions of bright sun and little or no cloud with the recorder not in shadow, the effect of occlusion would be slight, probably about 1 or 2% so long as the direct rays from the sun were not intercepted. The need for a correction for occlusion does not arise in estimating illumination below the surface in the Sörgat because the recorder and the collecting station suffered occlusion to a rather similar degree. For this reason and because of uncertainty as to the precise value, no correction has been applied.

(*c*) *Measurements of illumination*

The noon and midnight values of illumination shown by the recorder from 15 July to 26 August are given in Table 4 and Fig. 3. All values read from the recorder are referred to local apparent time obtained from watch time by correcting for the rate of the watch, longitude and equation of time. In Fig. 3 the occasions when the sun was shining have been marked by additional outer rings. The appropriate correction for reflection of diffuse light has been applied to all values; those for the majority of occasions with overcast or clouded sky are therefore approximately correct, while those for occasions with sunshine need a further correction for reflection which was applied in the following way. As observations under nearly cloudless conditions were rather few, additional values of illumination were read from the record at 1500, 1800 and 2100 h for occasions with the sun

shining unobscured (as noted by observation and as could be seen from the record) and the cloud cover was 0-2/10. All values thus obtained were plotted against the altitude of the sun (Fig. 4), a smooth curve was drawn through the points and the estimated corrections were applied to this curve. The corrected values are entered in Table 4, and broken curves showing the level of these corrected values have been drawn in Fig. 4 to show the true mean light intensity for sunshine with 0-2/10 cloud at noon and midnight according to the date. It is not possible to correct the sunshine values with 3-9/10 cloud precisely because the proportion of sky-light is uncertain. The correction applicable to conditions of 1-2/10 cloud is, however, a maximum and with more cloud the correction will become less as the sky-light increases until diffuse conditions are reached.

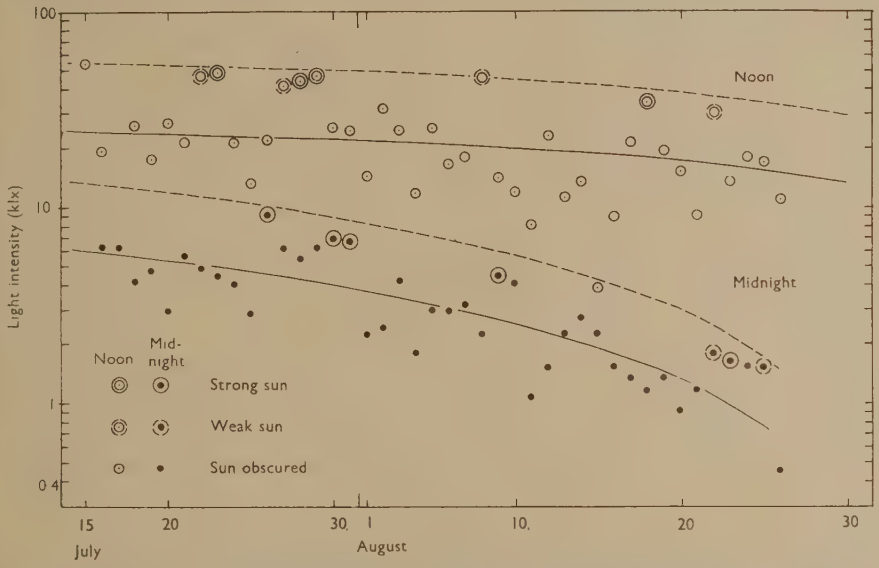

Fig. 3. Light intensity at midnight and noon, 15 July-26 August, with median curves (continuous lines) and curves for conditions of sunshine with 0-2/10 cloud (broken lines).

In considering the seasonal change in illumination the value of most significance to a marine animal is probably the mean or median on a logarithmic scale of intensity. This is shown in Fig. 3 where lines have been drawn through the midnight and through the noon illumination values. There are as many values of illumination above each of these lines as below, that is, they are median curves, and as they are approximately in the centre of each band of values they are also near the geometric mean. These median curves pass through values which are 0·45 times the estimated correct illumination under nearly cloudless skies. The curves of illumination under 0-2/10 cloud and the median curves through all the values show how the midnight values decline more rapidly than the noon values

so that the difference between night and day becomes greater as the season advances. On 15 July the midnight illumination is close to a quarter of that at noon; the fraction would be very similar on midsummer day with the sun 2° higher at noon and midnight, and by 25 August when the sun is very close to the horizon the fraction has become one-twentieth.

(*d*) *Estimation of illumination*

It is of interest to compare these observed values of illumination in Spitsbergen with the values which may be calculated from solar radiation, using the appropriate conversion factors. By far the most thorough treatment of illumination or solar radiation in these regions is that of Mosby (1932) in his work on the measure-

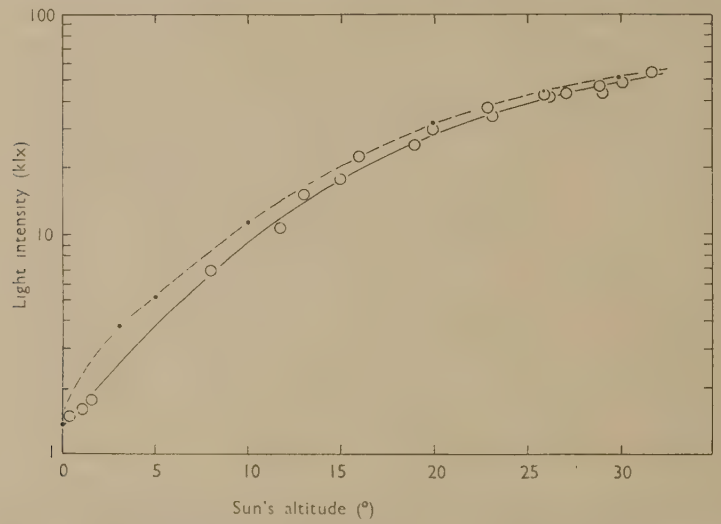

Fig. 4. Curve of the relation between light intensity and solar altitude for conditions of sunshine with 0-2/10 cloud at 0000, 1200, 1500, 1800 and 2100 h, with (broken line) a curve of intensity after applying a correction for the reflection of direct light.

ments made on the *MAUD* in her drift in the Polar Ocean off the north Siberian coast. Mosby used the formula developed by Linke (1922) which gives the direct solar radiation, Q_s, at sea level on a surface perpendicular to the sun as:

$$Q_s = Se^{Tm.am}$$

where T = the 'Trübungsfaktor' which represents the opacity of the atmosphere

$am = 0{\cdot}128\text{-}0{\cdot}054 \log m$

S = solar constant 1·932 cal cm^{-2} min^{-1}

m = air mass according to Bemporad (see Mosby).

The intensity on a horizontal surface is $Q_s \cos \theta$, where θ is the angle of incidence, and corrections are applicable for mean solar distance and air pressure. The total

Table 4. *Illumination above the sea surface*

All figures are in klx

	Midnight (LAT)*						Noon (LAT)					
	Midnight altitude of sun†	Observed minimum intensity	Observed intensity at midnight	Median curve	Corresponding intensity for sun and 0-2/10 cloud‡	Intensity with clear sky as estimated from solar radiation	Noon altitude of sun†	Observed maximum intensity	Observed intensity at noon	Median curve	Corresponding intensity for sun and 0-2/10 cloud‡	Intensity with clear sky as estimated from solar radiation
15 July	11° 09′			6·07	13·5	15·0	31° 44′	56·4	53·7	24·8	55	58·2
16 ,,		2·2	6·3					29·2	19·2			
17 ,,		4·5	6·3					22·4				
18 ,,		4·2	4·2					60·0	26·2			
19 ,,		4·5	4·8					62·5	17·4			
20 ,,	10° 17′	2·7	3·0	5·4	10·9	13·2	38° 57′	58·2	26·8	23·8	53	56·2
21 ,,		3·0	5·7					45·6	21·5			
22 ,,		5·0	5·0					65·5	46·6			
23 ,,		4·5	4·5					49·3	48·7			
24 ,,		3·9	4·0					65·4	21·3			
25 ,,		2·4	2·9					23·7	13·2			
26 ,,		5·4	9·1					45·6	21·9			
27 ,,		4·0	6·2					59·0	41·6			
28 ,,		4·9	5·5					46·5	43·8			
29 ,,		4·7	6·2					47·4	46·5			
30 ,,	8° 07′	5·4	6·9	4·0	8·9	9·7	28° 47′	35·8	25·5	22·5	50	51·0
31 ,,		6·3	6·7					30·4	24·6			
1 August		1·8	2·2					17·0	14·3			
2 ,,		1·5	2·4					50·1	31·8			
3 ,,		2·5	4·2					38·5	24·6			
4 ,,		1·5	1·8					16·6	11·8			
5 ,,		2·2	3·0					45·6	25·2			
6 ,,		3·3	3·0					19·5	16·5			
7 ,,		2·7	3·1					22·8	17·9			
8 ,,		2·2	2·2					55·5	45·6			
9 ,,		4·5	4·5					33·1	14·0			
10 ,,	5° 10′	0·72	4·0	2·6	5·7	5·3	25° 50′	35·8	11·9	19·8	44	44·7
11 ,,		0·90	1·1					18·7	8·1			
12 ,,		1·5	1·5					42·0	22·8			
13 ,,		2·2	2·2					14·4	11·2			
14 ,,		2·4	2·7					29·2	13·4			
15 ,,		1·6	2·2					19·7	3·8			
16 ,,		0·9	1·5					9·6	9·0			
17 ,,		1·3	1·3					27·8	21·2			
18 ,,		1·2	1·2					34·0	34·0			
19 ,,		1·1	1·3					25·9	19·2			
20 ,,	2° 02′	0·9	0·9	1·4	3·0	1·28	22° 42′	21·0	15·2	17·1	38	38·0
21 ,,		1·0	1·2					35·8	9·1			
22 ,,		1·8	1·8					31·0	30·0			
23 ,,		1·6	1·6					38·4	13·4			
24 ,,		0·6	1·5					33·2	17·9			
25 ,,	00° 21′	1·5	1·5	0·77	1·7	–	21° 01′	17·9	16·7	15·3	34	34·6
26 ,,		0·5	0·5					11·7	10·1			

* LAT, local apparent time (as would be shown by a sundial). † Not corrected for refraction. ‡ Corrected for reflection losses on basis of assumed proportions of direct and diffuse light.

radiation consists of this direct radiation together with the diffuse radiation from the sky. Mosby gives a series of values of the observed ratios of direct to total radiation which range from 0·40 at a solar altitude of 3° to 0·81 at a solar altitude of 40°. These values are very similar to those obtained by Kimball in America. The values of T yielded by the *MAUD* measurements and by those of Westman (1903) and Götz (1931) in Spitsbergen strongly suggest a figure close to 2·0 to be appropriate for this region for June, July and August. Accordingly, radiation on a horizontal surface at sea level at Sörgat has been calculated on the basis of $T = 2{\cdot}0$, using interpolated figures for the air mass according to Bemporad and using the solar constant of 1·96 cal cm^{-2} min^{-1}, less 3% as correction for mean solar distance. Corrections for air pressure and refraction have been omitted, and Mosby's observed ratio of direct to total radiation has been applied to give an estimate of total radiation. Solar radiation may be converted to light intensity by the appropriate factor. Kimball (1924) gave a series of these factors ranging from 7000 to 6200 ft candles per cal cm^{-2} min^{-1} for total radiation on a horizontal surface at solar zenith distances between 25° and 78·7°. Later values from Plymouth (Atkins & Poole 1936a) and Kew (Blackwell 1953, 1954, Blackwell, Eldridge & Robinson 1954) are in accord with these figures. Kimball's values have been used, interpolated for the correct solar altitude. The values of illumination estimated in this manner have been entered in Table 4; they show very good agreement with the observed values, showing that so long as a value of T may be assumed, the illumination in sunshine under a nearly cloudless sky may be estimated fairly closely.

(*e*) *The effect of cloud cover*

Having obtained corrected values of illumination corresponding to conditions of sunshine with 0-2/10 cloud, it is now possible to estimate the attenuation of light by cloud. The illumination for noon and midnight for occasions with overcast skies and with the sun completely obscured, as read from the record corrected for the angle of incidence of diffuse light, have been expressed as a percentage of the estimated correct illumination above the cloud, read from the broken curves of Fig. 3.

The results, from 15 July to 26 August are:

Midnight:	24 values; range 20·0-67·0%; mean 39·2%
Noon:	27 values; range 18·5-94%; mean 39·0%

These figures should, however, be adjusted for occlusion which cuts out about 5% of the light under overcast conditions and about 2% in sunshine. The adjusted mean figure for conditions of no occlusion is therefore 39+3% = 42%.

Illumination may be equated approximately with radiation; Mosby (1932), summarizing the radiation measurements from the *MAUD* expedition found the radiation income with overcast skies in 73° N to be 58%, compared with 29% from 40° N in America (Kimball's results). Ångström (1933) considered Mosby's arctic figure not to be strictly comparable because of reflection of diffuse radiation

from ground or sea surfaces covered with snow and ice, and calculated that if this were eliminated the value would be 35%, as against 23-24% at lower latitudes in the track of the cyclones. Ångström himself found the radiation on two practically clear days and fourteen perfectly cloudy days at 'Sveanor' in N. Spitsbergen to yield a figure of 41% for the transmission of overcast skies with a substantially non-reflecting ground surface, a figure very similar to that obtained in the Sörgat measurements; Olsson (1936b) obtained similar values from radiation measurements on the Isachsen plateau when adjusted to the case of no ground reflection. These Sörgat observations therefore supply additional evidence that the cloud layer is thinner in the polar regions than at lower latitudes, and in particular support Ångström's figure of roughly 40% for the average transmission of overcast skies in this area.

SURFACE LOSSES AND TRANSPARENCY

(*a*) *Secchi-disc observations*

Owing to the demands of time, it proved impractical to make photoelectric measurements of transparency on as many occasions as desirable. Transparency was therefore obtained from Secchi-disc measurements after comparison of Secchi-disc extinction depths and transparency on a number of occasions.

As in Scoresby Sound (Digby 1953) the disc was clipped to the wire passing over the stern of the boat and was raised and lowered several times for each observation, the depth of extinction being taken as the mean of the values for disappearance and reappearance. The disc was observed with the sky shaded by the head of the observer or by the side of the boat seen reflected in a wavelet, obviating much of the sky reflection which otherwise reduces the estimated depth by $\frac{1}{2}$-1 m (Table 2). Secchi-disc values ranged from 6·0 to 10·9 m in the Sörgat, with a value as low as 3·75 m at the station in Smeerenburgfjord. The values showed an increase of transparency during the period of observation (Fig. 5, Table 2), the approximate mean increasing from 6·5 m in mid-July to 9·5 m by 25 August.

The water was more turbid than at Scoresby Sound (Digby 1953) where Secchi-disc values ranged from about 10 m in mid-July to 15-20 m in August, September and October, with a single low value of 9·25 m at the end of August 1951 in close pack-ice. These values are probably not strictly comparable to values made from a larger boat, as will be described shortly, but they should indicate the seasonal trend reasonably accurately. Mosby (1938) found values of between 4 and 21 m to the north and west of Spitsbergen, with the lower values close to land (Treurenberg Bay and Hinlopen Strait). He found a decrease in transparency in the Hinlopen Strait from 21 to 4 m during summer, which he associated with hydrographic changes and a plankton increase over this period. Our observations in Scoresby Sound and the Sörgat covered a late phase of the plankton cycle during which the water incidentally became progressively clearer. This increase in transparency close to the coast during July and August is undoubtedly associated with the lessening of the load of silt brought down to the sea by melting streams as the air temperature falls. The extent to which the opacity of seawater is in

fact due to sediment or to the plankton and its associated particulate matter is, however, still an open question.

(*b*) *Photoelectric measurements*

Transparency of the water down to 30 m was measured by photoelectric apparatus on nine occasions. The apparatus comprised a sea cell, a deck cell and potentiometer, after the methods of Poole & Atkins (1934 a, b; 1937). The sea cell consisted of a 3·5 cm diameter EEL barrier-layer photocell mounted in a watertight gunmetal housing similar to that described by Gall (1949) and covered by a light green gelatine filter (Ilford 41/43) to correct the response of the photocell to that of the human eye below the window of the cell, and a flashed opal above it.

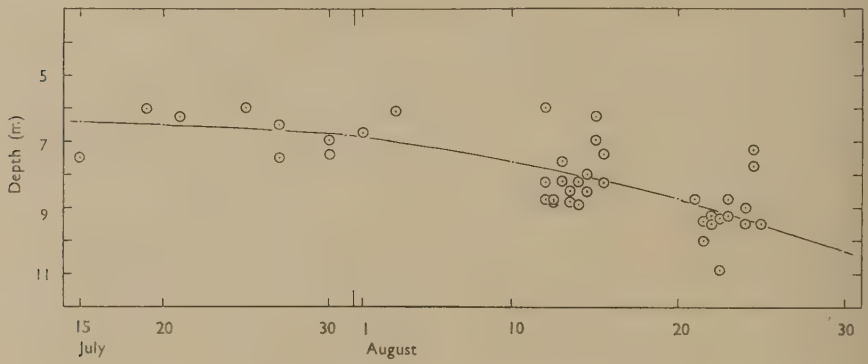

Fig. 5. Secchi-disc extinction depths with approximate mean curve.

The filter and opal reduced the light falling on the cell to about one-tenth, and with a 200 ω shunt the output of the cell was linear with illumination to above 1·5 klx incident light, corresponding to 15 klx falling on the opal: conditions for linearity were observed by using the cell with filter and opal alone up to 10 klx and inserting an extra neutral filter (Chance ON 31, about 25% transmission) for higher intensities.

The deck cell consisted of a similar photocell shunted by a 200 ω potentiometer winding and covered by a suitable neutral filter and an opal. The output of the sea cell was compared with that of the deck cell or with a fixed potential by means of the potentiometer, an interrupter and an amplifier, the null-point being found by earphones. A very serviceable and compact amplifier for this purpose was provided by a modified three valve hearing aid set mounted in a small box together with batteries, potentiometer and shunts.

The sea cell was suspended from a boom 2 m from the side of the boat. A first reading was taken above the water surface after immersion to displace air from the spaces between the cell window and opal. Subsequent readings were taken just below the surface and at intervals of 2 m to 25 or 30 m depth. Subsurface readings

were multiplied by the factor 1·09 calculated by Atkins & Poole (1933) for photometers of this type to correct for various complex reflections effects which occur when the cell is submerged.

A typical curve of illumination with depth is shown in Fig. 6. The features are familiar; on lowering to just below the surface the illumination decreased because of surface film losses, often termed reflection but probably more complex. On lowering the cell further, illumination decreased more rapidly at first and then less rapidly. In the Sörgat, the logarithm of the light intensity was strictly proportional to depth below about 4 m. The curvature of the relation between the logarithm of the light intensity and depth near the surface is well known and appears in almost all the published figures of work of this nature; it is complex in origin and probably arises partly from the changes of angular distribution of the

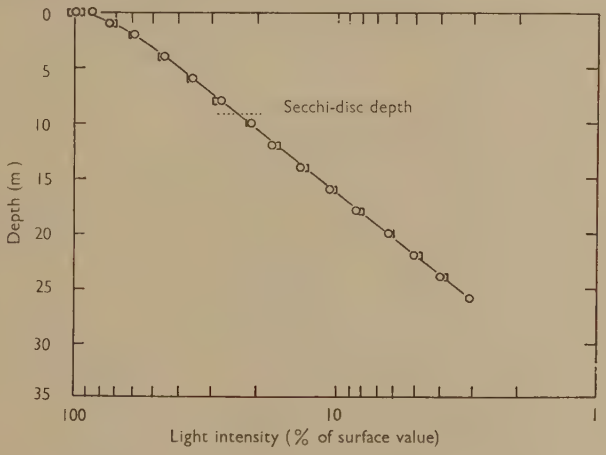

Fig. 6. Typical curve of attenuation of light with depth (Series 6) in the Sörgat.

light rays with depth, partly from selective absorption of the longer wavelengths, and partly from real changes in the content and properties of the seawater.

The nine series of readings gave very similar results (Table 5). Losses at the surface film varied from 14% to 20% (average 17·5%) under the usual overcast conditions; a single observation in bright sunshine gave a value of 30%. The opacity of the water as defined by the vertical extinction coefficient K is given by

$$K = \frac{2{\cdot}30}{d}\,(\log_{10} I_z - \log_{10} I_{z+d})$$

where I_z and I_{z+d} represent the light intensities at depths z and $z+d$ m. The mean extinction coefficient, K_{0-20}, for the depth interval 0-20 m, which includes the zone of curvature, was 0·144, compared with 0·129 for the interval 10-25 m, where the exponential relation held good.

Table 5. *Photoelectric measurements of transparency*

	Surface film losses (as % of above-surface light)	K_{0-20}	$K_{10\cdot25}$	Secchi-disc extinction depth, D (m)	Illumination at which Secchi-disc disappears (as % of above-surface light)	$K_{0-20} \times D$	$K_{10-25} \times D$	Sky and sea surface
12 August	19	·141	·134	8·8	21·2	1·24	1·18	Overcast, surface rippled
13 ,,	18	·144	·131	8·2	22·3	1·18	1·07	Overcast, glass calm
13 ,,	19	·138	·118	8·8	18·5	1·21	1·04	Overcast, surface rippled, light rain
14 ,,	20	·142	·140	8·9	22·3	1·26	1·25	Overcast, surface rippled
15 ,,	18	·159	·141	7·0	21·2	1·11	0·99	Overcast, wavelets
21 ,,	14	·156	·123	9·7	22·3	1·51	1·19	9/10 stratus, very weak low sun, snow, surface rippled
22 ,,	30	·129	·119	9·3	19·6	1·19	1·10	3/10 stratus, bright sun, surface rippled
22 ,,	17	·141	·129	9·3	19·4	1·31	1·20	8/10 thin stratus, weak sun, surface rippled
24 ,,	15	·144	·124	9·2	23·4	1·32	1·14	9/10 stratus, sun obscured, wavelets
Mean	17·5 (excluding high value in bright sunshine)	·144	·129	8·8	21·1	1·26	1·13	

The Secchi disc disappeared at a depth at which the above-surface light was reduced to 18·5-23·4% (mean 21·1%), or below-surface light to a mean of 25·6%. The disc disappeared at a shallower depth for a given transparency than is usually assumed. The often-quoted figure for the product of the Secchi-disc depth and the extinction coefficient, K_{0-20} (by which K_{0-20} may be obtained roughly if the Secchi-disc depth is known) is 1·7 (Poole & Atkins 1929). The figure obtained from these observations, for the same depth interval, is 1·11-1·51 (mean 1·26) and that for the depth interval 10-25 m, below the zone of curvature, is only 1·13. This difference probably arises from the method of observation. A rowboat or small motorboat does not shade the surface water and absorb the scattered light responsible for the extinction of the disc to such an extent as does a larger vessel. The disc readings, when made close to a large vessel, will in fact be intimately dependent on its size and proximity.

The relation between transparency and the Secchi-disc readings found in the Sörgat probably also hold good for the observations in Scoresby Sound in 1950-1, by identical methods (Digby 1953).

DERIVATION OF SUB-SURFACE ILLUMINATION FROM SECCHI-DISC OBSERVATIONS

The transparency of the surface layers is not wholly satisfactory for calculating the depths of the isolumes in deeper water, because of the curvature of the relation between the logarithm of light intensity and depth just below the surface (Fig. 6). It seems reasonable, however, to assume that the vertical extinction coefficient in the upper few metres stands in proportion to that below this depth, and with this assumption we may relate the transparency above the Secchi-disc level to that below it. The expression of transparency which is of direct interest for biological purposes is not so much the extinction coefficient, which is the reciprocal value of the distance for reduction of illumination to 0·368 of its value but the distance for reduction to one-tenth, which is numerically equal to $2{\cdot}30/K$. This depth interval in the region below the surface few metres may be read directly from the graph of each series of transparency measurements and may be related directly to the Secchi-disc depth (Fig. 7). A mean Secchi-disc depth of 8·8 m corresponds to a mean depth increment of 18·0 m (almost exactly twice the Secchi-disc depth) for a reduction of light to one-tenth in this region below the surface curvature.

The depth at which a particular light intensity is found on a number of different occasions may then be obtained simply and rapidly from the disc measurements and above-surface light intensity by a graphical method. Taking the Secchi-disc depth as that to which 21·1% of the above-surface light penetrates, a family of standard curves of attenuation of light with depth for different Secchi-disc values was drawn out on log-normal graph paper (Fig. 8). Each curve consisted of a straight line passing through the value of 21·1% of the above surface light at the Secchi-disc depth and of 2·11% at a depth greater than this by the appropriate depth increment for decrease of light to one-tenth, as read from Fig. 7. Each line

was produced from 4 m as a smooth curve to meet the surface at 82·5% of the above-surface light, to allow for the mean surface film loss of 17·5%. The depth of a particular isolume was obtained by expressing the illumination as a percentage

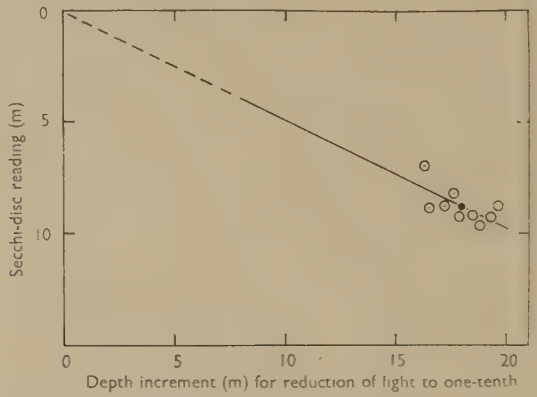

Fig. 7. Relation of the Secchi-disc depth to the depth increment for reduction of light to one-tenth, below the 4 m level.

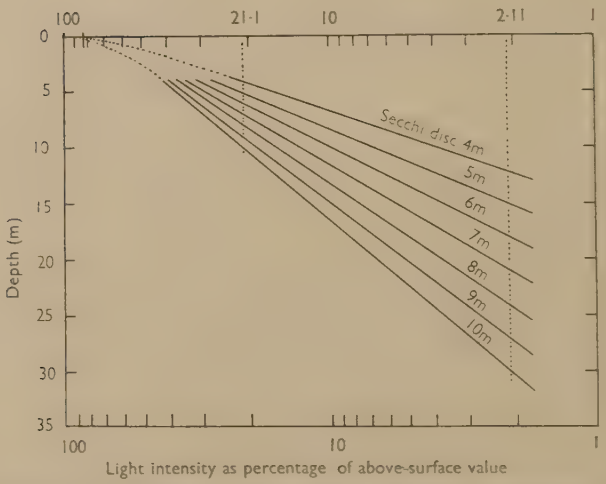

Fig. 8. Family of standard curves for the attenuation of light with depth for various Secchi-disc values.

of that above the surface and reading off the depth corresponding to that percentage from the curve for the appropriate Secchi-disc value. Depths of lower isolumes were obtained by the addition of appropriate increment of depths. The isolumes for 1·0, 0·1 and 0·01 klx at noon and midnight throughout the season were plotted

in this manner, taking as value of above-surface light the points of the mean curves of Fig. 3.

The changes in sub-surface light obtained in this manner (Fig. 9) show that although the light at the surface decreased slightly throughout late July and August, that at depths below about 15 m at noon and 30 m at midnight increased owing to the increased transparency. Over the period from mid-July until late August, the vertical excursion of the isolumes from noon to midnight (shown by the arrows) increased from under 10 to nearly 30 m. Consideration of the errors involved in this treatment shows that these are relatively slight. An error of 20% in the estimation of surface loss would result in an error in the depths of the isolumes of 1 m and 2 m with Secchi-disc depths of 6 m and 10 m respectively. The errors arising from the estimation of transparency from Secchi-disc observations are the greatest; apart from the assumptions mentioned earlier the spread of

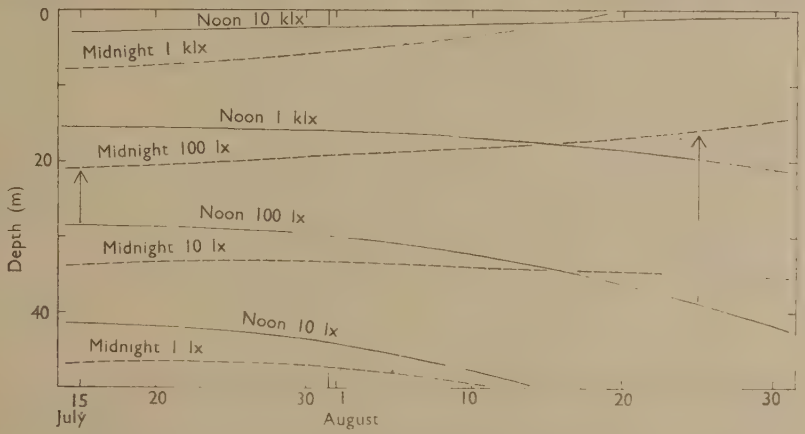

Fig. 9. Median position of isolumes at noon and midnight. Arrows show the extent of diurnal movement of the isolumes on 15 July and 25 August.

points in Fig. 6 shows that for an observed Secchi-disc depth of 9 m the depth increment of 18·2 m for reduction of light to one-tenth may be 2 m greater or less. This effect is cumulative with depth, and would amount to an error of up to 6 m in the position of an isolume at 50 m. In view of the vertical spread of plankton animals through zones of greatly differing light intensity, this may be regarded as not of great importance.

DISCUSSION

It is of interest to consider the relative importance of solar altitude, cloud cover and transparency on light intensity below the surface. In the north of Spitsbergen at midsummer the diurnal changes of solar altitude result in the midnight illumination being one-quarter of that at noon; as the season advances the difference becomes greater and by 25 August when the sun is just above the horizon at night, the fraction is about one-twentieth. In late summer as the skies are usually

overcast and the light diffuse, the extent of the diurnal changes of illumination below the surface of the sea will be similar to those above it. Under glass-calm conditions with cloudless skies the difference between day and night below the sea surface will be greater because of the greater Fresnel reflection of the direct rays of light from the low sun at night. No measurements of light penetration have so far been made under these conditions, but since at a solar altitude of 10° 45% of the radiation, corresponding to a greater proportion of visible light, is diffuse, roughly half the total light falling on the sea surface will still penetrate even if the direct ray were completely reflected.

During June and July cloud cover may reduce the light intensity found with bright sunshine to one-quarter or one-fifth, a change comparable in magnitude to that arising from the diurnal change of solar altitude. A reduction of illumination by almost this amount can result from differences in cloud thickness under completely overcast skies. Change of cloud cover may therefore double or cancel out the effect of the diurnal change in solar altitude during these months. The extent of attenuation of light by overcast skies is practically independent of the altitude of the sun and does not alter significantly during July and August, during which time the diurnal changes of solar altitude become greater.

Change of above-surface light by a factor of four times, the mean diurnal change in midsummer, will cause vertical displacement of the isolumes just below the sea surface by 3 m and 8 m for Secchi-disc readings of 4 m and 10 m respectively. If plankton animals were to follow these isolumes closely they would clearly not make extensive migrations. The numbers at or just below the surface, however, might well be expected to show a substantial change, sufficient to affect their visibility from the deck of a boat and their availability as food for surface-feeding sea birds. Bogorov (1941, 1946) has described such changes in the numbers of copepods at the surface in the southern White Sea the vertical distribution being otherwise constant. If, however, a sunny day were followed by a night with dense cloud over the clearer water offshore, with Secchi-disc depths down to perhaps 20 m (Mosby 1938) the isolumes even in midsummer would be displaced upwards by 40 m, and an obvious migration to the surface might be expected. Walter's observation of medusae moving from depths of 30 m and more up to the surface at night in the Hinlopen straight in north Spitsbergen (Russell 1927), where Mosby (1938) later found Secchi-disc values of up to 21 m, are therefore quite in keeping with the possible displacement of the isolumes.

The variation of transparency locally where melt-water reaches the sea will cause great differences in submarine illumination. Hartley & Dunbar (1938) have described the way in which euphausids and other plankton animals come to the surface in a 'light-tight' zone formed by turbid melt-water at the ends of glaciers. Similar sheets of turbid fresh water spread out from the rivers in the Arctic in calm weather. These conditions were not, however, seen in the Sörgat.

The influx of suspended material in summer will result in rather complex patterns of seasonal changes of light intensity in coastal arctic waters. In the vicinity of the mouths of the larger streams there will be a rapid alternation of

light and dark conditions below the surface related to the factors which affect the rate of melting on land, and to the wind and tide which move the turbid surface layers from one place to another. In coastal localities in general at depths of 50 m or more, there are probably two periods of maximum light intensity during the year, spring and autumn. Light will be at a minimum in winter when it is dark above the surface, and increase in spring as the sun rises above the horizon. As the melt sets in and turbid streams add their load of sediment to the sea, light at depth will become reduced by the sediment, and will increase again in the late summer and autumn (as shown by these observations in the Sörgat) before finally decreasing towards the winter minimum.

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SUMMARY

1. Measurements of illumination and its penetration into the sea were made in the Sörgat, N.W. Spitsbergen, from mid-July until late August 1956. The observations were made as part of a study of the vertical distribution and movements of plankton animals under arctic conditions.

2. Skies were overcast for most of the time. The occasions with sunshine and up to 2/10 cloud allowed illumination to be related to the altitude of the sun. The light intensity on a horizontal surface at noon under these conditions declined from 55 klx on 15 July to 34 klx on 25 August, while the similar midnight values decreased from 13·5 to 1·7 klx over the same period. The midnight illumination with nearly cloudless skies therefore declined from 25% to 5% of the corresponding noon values over this period. These values agree well with those that may be arrived at by calculating solar radiation intensity and converting to illumination by the appropriate factor.

3. Cloud cover reduced illumination, half the observations lying below 45% of the corresponding maxima. The mean light transmission for overcast skies was 39%.

4. The mean depth for extinction of the Secchi-disc increased from 6·5 m on 15 July to 9·5 m on 25 August.

5. Photoelectric measurements of transparency showed the surface losses to average 17·5% under overcast skies. Light intensity below 4 m decreased exponentially with depth. As used in the Sörgat the Secchi-disc disappeared at a mean value of 21·1% of the above-surface illumination. The extinction coefficient, K, below 4 m was related to the Secchi-disc D by $K = \frac{1{\cdot}13}{D}$, the depth interval for decrease of light to one-tenth being twice the Secchi-disc depth.

6. A method is described for estimating sub-surface light intensity from measurements of above-surface intensity and Secchi-disc observations.

7. Light intensity a short way beneath the surface decreased between 15 July and 25 August, but because of the increasing transparency, the intensity at 15-30 m remained constant, while below this level illumination increased.

8. The changes of illumination are discussed in relation to their significance to plankton animals in the Arctic.

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THE FOOD CONSUMPTION OF DIFFERENT INSTARS OF *MITOPUS MORIO* (F.) (PHALANGIDA) UNDER NATURAL CONDITIONS

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(With 1 Figure in the Text)

Before a reliable picture can be formed of energy transformations within a community, more information must be available on the efficiency with which animals in nature utilize their food materials. The present paper extends the study of Phillipson (1960) on the utilization of food by adults of *Mitopus morio* (F.) to a study of food utilization throughout the whole of this organism's life history. It presents results on the percentage assimilation of food in the laboratory, and the amount of energy obtained by *M. morio* from its food at various stages of its life history under natural conditions.

ASSIMILATION OF FOOD

(*a*) *In the laboratory*

Instars of *M. morio* can be separated on femur length of the second walking leg (B. Heighton, personal communication). The relevant measurements are given in Table 1.

Table 1. *Determination of the instars of* Mitopus morio *by femur length of the second walking leg*

Instar	Length of F_2 (mm)	Instar	Length of F_2 (mm)
II	0·43-0·81	V	1·68-2·35
III	0·81-1·20	VI	2·35-3·59
IV	1·20-1·68	VII	>3·59

Although *M. morio* can be considered a general predator, one of the factors governing the capture of food is prey size (Phillipson 1960). Observation of juveniles in the field showed them to eat a variety of small organisms, but Collembola and nymphs of Heteroptera were the most frequent source of food. In the laboratory, experimental animals were kept separately in circular glass dishes $15 \times 7{\cdot}5$ cm sealed by a glass plate. The bottom of each dish was covered by a filter paper kept moist by water from an inverted 2×1 in. glass tube. When fed on Collembola, *Tomocerus minor* (Lubbock) or *Isotoma viridis* (Bourlet), faecal pellets ranging in colour from black to green were produced. When cercopid nymphs were the food source, pink or red faeces appeared. Thus faeces produced from a given food could be identified.

Animals brought into the laboratory were starved for 24 h and the colour of the faeces noted. They were then given food that produced faeces of a different colour. After a further 24 h food that produced faeces of the first colour observed was given. It was during this last period that measurements were made of the initial live weight of the food, the weight of food remains after feeding, the weight of faeces of appropriate colour produced, and the live weight of the experimental animal. The weight of faeces produced was calculated indirectly by the volume method described by Phillipson (1960). In the results all weights other than the live weight of *Mitopus* are expressed as dry weights. Since no large increase in weight of the experimental animal occurred during the experimental period, the following equations were applied to the measurements obtained:

1. Weight of food eaten = weight of food —weight of food not eaten.
2. Weight of non-assimilated food = weight of faeces.
3. Weight of food assimilated = weight of food —weight of non-assimilated food.
   = weight of food eaten —weight of faeces.

Table 2 shows the summarized results of the amount of food assimilated. No

Table 2. *Amount of food assimilated by* Mitopus morio *expressed as a percentage of the weight of food eaten* (*dry weights*)

Instar	Amount eaten (mg)	Faeces (mg)	Percentage assimilation
II	0·129	0·035	74 ±1·0
III	0·229	0·095	59 ±4·3
IV	0·357	0·162	55 ±4·3
V	1·069	0·484	55 ±5·5
VI	1·539	0·862	44 ±5·2
VII	From Phillipson (1960)		47

data are available for instar I as this stage lasts only 2-3 h at the most. At least twenty individuals were used for each of the categories noted.

(*b*) *In nature*

Collections of *M. morio* were made at 05, 11, 17 and 23 h GMT on each of the days 5 May, 6 June and 6 July 1959. Each animal was isolated for 24 h and after this period the instar was determined along with the weight of faeces produced. The four collections during each 24-hour period were an attempt to even out any irregularities in faeces production that might arise from a periodicity in defaecation. At least twenty individuals of each of the instars II-V were examined in this way and twenty of each sex for instars VI and VII (July). The data thus obtained gave the average faeces production per animal per 24 h, and from this, using the percentage assimilation data found in laboratory experiments, the weight of food eaten and the weight of food assimilated per 24 h in nature could be calculated. Table 3 shows the results obtained. The sharp rise in weight, faeces

production, food consumption and assimilation in the later instars of the females seems to be connected with the development of eggs (Fig. 1). The similar but less marked increase shown by males is also probably connected with sexual activity. The decreases shown by the adult instars in September can be attributed to senescence.

M. morio feeds mainly on insects, therefore by using the calorific value of 'mixed insects' as 5·82 Kcal/*g* dry matter (Gibb 1957) and the figures in Table 3, the energy obtained from food by the various instars was calculated (Table 4). This gives

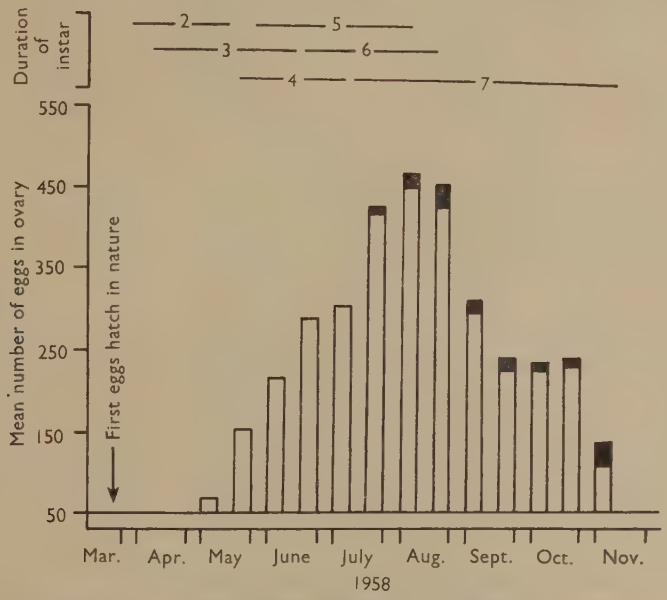

Fig. 1. Reproductive cycle of female *Mitopus morio*. Each column the average of 10 animals; □ immature eggs, ■ mature eggs.

an actual rather than relative estimate of energy turnover by the different developmental stages at different times of the year.

THE CONSUMPTION QUOTIENT OR VAN DER DRIFT CONSTANT

It has been generally accepted that food consumption, an approximate measure of metabolic activity, is directly proportional to the surface area of the consumer in different sized adult Diplopoda and Isopoda (Van der Drift 1951, Gere 1956, Dunger 1958). The relationship of food consumption to surface area is expressed as $c/\sqrt[3]{g^2}$ where c = dry weight of food consumed in unit time and $\sqrt[3]{g^2} \doteq$ surface area of the animal, g being its live weight; Gere (1956) expresses g in terms of absolute dry weight. This expression has been called 'the Van der Drift Constant' by Balogh (1953) and Gere (1956), whereas Dunger (1958) prefers the term 'Konsumquotient' (KQ) and uses the formula $KQ = 100c/\sqrt[3]{g^2}$. In the present

Table 3. *Food consumption, assimilation and faeces production per 24 h by* Mitopus morio *under natural conditions*

Instar	Mean live weight of *M. morio* (mg)		Dry weight of faeces (mg)		Dry weight of food consumed (mg)		Dry weight of food assimilated (mg)	
II	1·0 ±0·1		0·0207 ±0·0066		0·0796 ±0·0254		0·0589 ±0·0188	
III	1·7 ±0·1		0·0431 ±0·0029		0·1051 ±0·0071		0·0620 ±0·0042	
IV	3·6 ±0·4		0·0483 ±0·0057		0·1073 ±0·0127		0·0590 ±0·0070	
V	6·0 ±0·4		0·1620 ±0·0228		0·3600 ±0·0507		0·1980 ±0·0279	
	males	females	males	females	males	females	males	females
VI	11·5 ±0·7	17·0 ±0·4	0·2430 ±0·0426	0·5522 ±0·0369	0·4339 ±0·0761	0·9861 ±0·0659	0·1909 ±0·0335	0·4339 ±0·0290
VII (July)	26·0 ±1·3	66·7 ±3·0	0·2711 ±0·0236	0·4092 ±0·0527	0·5115 ±0·0445	0·7721 ±0·0994	0·2404 ±0·0209	0·3629 ±0·0467
VII (September)	23·0 ±1·1	50·0 ±4·6	0·0596 ±0·0054	0·2916 ±0·0172	0·1125 ±0·0102	0·5494 ±0·0325	0·0529 ±0·0048	0·2578 ±0·0153

study Dunger's nomenclature is followed. Van der Drift (1951), using food consumption as an index, showed that in mature Diplopoda of different sizes, with the exception of the largest animals, the amount of leaf litter consumed was fairly proportional to surface area. He realized, however, that fluctuations in temperature and humidity might influence food consumption, and concluded that the effect of these fluctuations should be investigated before using food consumption

Table 4. *Calorific equivalents of food consumed, food assimilated, and faeces produced per 24 h by* Mitopus morio *under natural conditions*

Instar	Mean live weight of *M. morio* (mg)		Faeces (cal)		Food consumed (cal)		Food assimilated (cal)	
II	1·0		0·120		0·463		0·343	
III	1·7		0·251		0·613		0·361	
IV	3·6		0·281		0·624		0·343	
V	6·0		0·943		2·095		1·152	
	males	females	males	females	males	females	males	females
VI	11·5	17·0	1·414	3·214	2·525	5·739	1·111	2·525
VII (July)	26·0	66·7	1·578	2·382	2·977	4·494	1·399	2·112
VII (September)	23·0	50·0	0·347	1·698	0·655	3·198	0·308	1·500

as a quantitative index of metabolic activity. Gere (1956) used the 'constant' in studying Diplopoda and Isopoda and showed that under identical, but not necessarily constant, conditions its constancy was independent of size. Furthermore, he showed that it could be used to compare the metabolic activity of different species. Dunger (1958) with more intensive work on Diplopoda and Isopoda showed that the Van der Drift Constant or Konsumquotient (*KQ*) as he preferred

Table 5. *The amount of food consumed and assimilated in 24 h per unit weight by different instars of* Mitopus morio

Instar	Dry weight of food consumed (mg per mg live weight)		Dry weight of food assimilated (mg per mg live weight)	
II	0·0796 ± 0·0254		0·0589 ± 0·0188	
III	0·0618 ± 0·0042		0·0365 ± 0·0025	
IV	0·0298 ± 0·0035		0·0164 ± 0·0019	
V	0·0600 ± 0·0085		0·0330 ± 0·0047	
	males	females	males	females
VI	0·0377 ± 0·0066	0·0580 ± 0·0039	0·0166 ± 0·0029	0·0255 ± 0·0017
VII (July)	0·0197 ± 0·0017	0·0116 ± 0·0015	0·0092 ± 0·0008	0·0054 ± 0·007
VII (September)	0·0049 ± 0·0004	0·0110 ± 0·0007	0·0049 ± 0·0004	0·0052 ± 0·0003

to call it, varied with environmental conditions, animal species and quality of food, thus disagreeing in part with Gere (1956). He did conclude, however, that the *KQ* was independent of size and age within a species. Furthermore he showed that the *KQ* could be calculated within certain limits by substituting faeces production in the place of food consumption. Table 5 shows clearly that food consumption and assimilation were not directly proportional to the weight of

Table 6. *Consumption quotients for different instars of* Mitopus morio

Figures show the values of *KQ* calculated: A, from the dry weight of food consumed; B, from the dry weight of faeces produced; C, from the dry weight of food assimilated. Levels of significance (P) are shown in parentheses.

Instar	A		B		C	
II	7·96 ±2·54		2·07 ±0·66		5·89 ±1·88	
	(ns)		(0·02)		(0·02)	
III	7·38 ±0·50		3·03 ±0·20		4·35 ±0·09	
	(0·001)		(0·01)		(0·001)	
IV	4·57 ±0·54		2·06 ±0·24		2·51 ±0·30	
	(0·001)		(0·001)		(0·001)	
V	10·90 ±1·53		4·91 ±0·69		5·99 ±0·84	
	males	females	males	females	males	females
	(0·01)	(0·001)	(ns)	(0·001)	(0·001)	(ns)
VI	8·52 ±1·19	—(0·001)— 14·51 ±0·99	4·77 ±0·84	—(0·001)— 8·35 ±0·51	3·75 ±0·66	—(0·001)— 6·56 ±0·44
	(0·001)	(0·001)	(0·001)	(0·001)	(0·01)	(0·001)
VII (July)	5·83 ±0·51	—(0·02) — 4·70 ±0·60	3·09 ±0·27	—(ns)— 2·49 ±0·32	2·74 ±0·24	—(ns)— 2·21 ±0·28
	(0·001)	(ns)	(0·001)	(ns)	(0·001)	(ns)
VII (September)	1·39 ±0·13	—(0·001)— 4·05 ±0·24	0·74 ±0·07	—(0·001)— 2·15 ±0·13	0·73 ±0·06	—(0·001)— 1·90 ±0·11

M. morio. Calculations of the consumption quotient for all instars studied are shown in Table 6.

DISCUSSION

The estimates of metabolic activity of different instars of *Mitopus morio* obtained in the present study were calculated in terms of the dry weight of food assimilated and are convertible to calorific values, thereby giving an actual estimate of energy turnover by the animal under natural conditions. Other methods of measuring metabolic activity in order to calculate energy turnover by different animals have been used. Bornebusch (1930) assumed that the 'surface law' applied to his animals and therefore that respiration was proportional to $\sqrt[3]{\text{weight}^2}$. Using the average respiration of a gram individual at 13° C as a measure of metabolic activity and the monthly mean temperatures of the habitats studied, he compared the intensity of metabolism in different habitats. Among others, Van der Drift (1951) has criticized Bornebusch on the grounds that too many suppositions and approximations were made for the results to be of much value. Nielsen (1949) has used laboratory respiration studies as an index of metabolic activity in different nematode groups. As pointed out by him the method has attendant disadvantages, although despite the disadvantages, respiration studies can be an important ecological tool for studying organisms too small to be handled readily in any other way. For larger organisms units other than oxygen consumption have been used as a measure of metabolic activity by Van der Drift (1951), Gere (1956) and Dunger (1958).

The present investigation demonstrates that for phalangids the expressions $c/\sqrt[3]{g^2}$ and $e/\sqrt[3]{g^2}$ cannot justifiably be described as a 'constant' either within the same size-group or between different age or developmental stages. In all three estimates of the KQ (Table 6) an increase in metabolic activity is evident in instars V and VI (female) and coincides with the immediate pre-reproductive period (Fig. 1). This situation is comparable with one found by Berg, Jørgen & Ockelmann (1958) in *Ancylus fluviatilis* (O. F. Müller), where an increase in respiration occurred just before the reproductive season. The lowering of metabolic activity in the adult instar of *Mitopus morio*, also noted in Isopoda and Diplopoda (Van der Drift 1951, and Gere 1956) can be attributed to senescence. The high metabolism in instar II, apparent only in the figures for KQ estimated from food consumption and food assimilation, can be compared with the relatively high oxygen consumption found in young worker bees over the first 2 days after emergence (Allen 1959). Both Berg's work and the present investigation demonstrate clearly that metabolic activity does not bear a simple relationship to surface area but varies with the physiological state of the animal. Zeuthen (1955) obviously felt this when he stated that most organisms studied from the point of view of metabolic activity are studied in comparable physiological states and that such values as are recorded are measured over a relatively narrow range of body size.

Clearly respiration and KQ studies can only give reliable estimates of energy

turnover by an animal species when that species has been studied in all stages of its life history and the seasonal fluctuations of the environment are known. The present method of estimating the metabolic activity of readily handled organisms has distinct advantages over respiration and KQ studies in that it measures what happens in nature, is independent of 'surface law' and fluctuating environmental conditions. The method has brought to light another point about the feeding biology of *Mitopus*. The early stages assimilated a much higher proportion of consumed food than later instars (Table 2). The high percentage assimilation of instar II (74%) is of the same order as that of *Ephestia kuehniella Z.* caterpillars (Gere 1951), which was attributed to the efficient combustion of dry food to supply metabolic water. This explanation is unlikely to apply to *Mitopus morio* because of the relatively high water content of its food. Observation has shown that the chelicerae of early instars are too weak to tear up the hard parts of the prey. Thus food entering the gut, since it is mainly fat body and muscle, has a higher proportion of digestible material than that entering the gut of later instars. It also demonstrates that animals apparently eating the same food organism need not necessarily be eating the same constituents of such organisms.

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SUMMARY

1. The amount of food assimilated, expressed as a percentage of the weight of food eaten, by different instars of *Mitopus morio* was highest (74%) in instar II and fell to 47% in the adult.

2. Food consumption under field conditions ranged from 0·463 cal day in instar II (average live weight, 1 mg) to 2·977 cal day in an adult male (average live weight 26 mg) and 5·739 cal day in a VI instar female (average live weight 17 mg). The corresponding average calorific values for food assimilated per day ranged from 0·343 cal in instar II to 1·399 cal in an adult male and 2·525 cal in VI instar females.

3. The amount of food consumed per mg live weight of *M. morio* per 24 h decreased from 0·079 mg (dry weight) in instar II to 0·005 mg in adult males and 0·011 mg in adult females. The corresponding amounts of food assimilated per mg live weight decreased from 0·059 mg in instar II to 0·005 mg (dry weight) in both adult males and females.

4. Metabolic activity measured by substituting food consumption or food assimilation or faeces production for c in the expression $c\sqrt[3]{g^2}$, where $\sqrt[3]{g^2}$ represents the surface area of the animal, was not approximately constant, and therefore not directly proportional to the surface area of *M. morio*. The 'constant' was affected by the physiological state of the animal.

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MORPHOMETRIC STUDIES OF THE DESERT LOCUST, *SCHISTOCERCA GREGARIA* (FORSK.)

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(With 8 Figures in the Text)

This paper is concerned with the comparative analysis of samples of adults of the desert locust (*Schistocerca gregaria* Forsk.) from populations for which the densities and other environmental conditions during development were known in some detail.

The shape of an animal, of which morphometrics are a numerical expression, is dependent upon genetically transmitted characters and the modifying influence of the environment on them. Environmental factors may be conveniently classified as density-dependent, including factors directly associated with the number of individuals per unit area or unit volume of habitat, and density-independent, including conditions of the physical surroundings such as the habitat and its micro-climate.

The desert locust is a markedly nomadic animal, both in swarms and in low-density populations. Studies on the behaviour and ecology of this insect are often necessarily incomplete because it is generally not possible to have positive knowledge of density, history and conditions of development of a given population before the time of first observation at any particular locality and season. The work of Waloff (1946), Rainey & Waloff (1948) and Rainey (1951), demonstrating downwind displacements of swarms of the desert locust, is of importance in permitting determinations of possible sources of populations by tracing back movements in relation to wind trajectories. Such deductions concerning population histories can be supplemented with information provided by any measurable morphological characters that may be related to the density and other environmental conditions of populations during pre-adult development.

THE MORPHOLOGICAL CHARACTERS MEASURED

The measurements were carried out by five different observers using vernier callipers, scaled to 0·1 mm, and calibrated to the same standard. Individual observers' errors of both bias and variability were discounted because they were negligible compared respectively with the differences of sample mean morphometrics and the sample variability. Three characters were used: elytron length (*E*), femur length (*F*), and head width (*C*). The measurements were made in the way described in some detail by Dirsh (1953). The proportion in a sample of adults having six or seven vertical eye stripes has been used as a phase character

by Roonwal (1945). Observations on the number of eye stripes in four of the samples studied have indicated that this character is of some value in assessment of population history from morphological characters. This paper will be mainly concerned, however, with the three morphometric characters given above. It will be shown that these characters, within the limits of the data obtained, may be used to discriminate to some degree between adults of different histories. The need for measurement of other characters, amongst which eye stripes may be of importance, in order to obtain better discrimination, will be discussed.

THE POPULATIONS STUDIED

The samples used were taken from a total of fourteen populations of which three were from the same locality at different seasons (Table 1). The remaining eleven populations were from different localities; three of these were obtained in early 1950, two in August-September 1953, and the remaining six were obtained during different seasons. Samples of adults known to be the parents of particular fledglings were obtained on five occasions. Similar data were obtained for a population of mature adults that were very probably the parents of one population studied, and information on the probable morphometric characters of the parent adults was available for five further cases. In all the above instances there was evidence of the behaviour of the parent adults, as there was also in the case of one of the three remaining, but less well documented, populations. No completely reliable evidence was obtained for either the morphometrics or the behaviour of the parents of two of the populations studied.

For convenience of description, in the early sections of this paper where the morphometric characters of adults, particularly in respect of the ratios $E : F$ and $F : C$, are such as to be considered generally typical of non-swarming and swarming populations (Dirsh 1953), the terms *solitariform* and *gregariform* (Pasquier 1952) will be used.

The histories of the fourteen populations may be summarized as follows:

1. Akbanazuf, Eritrea (15° 53′ N, 39° 15′ E), January-March 1950.

A sample of adults collected in this area, which quite reasonably were presumed to be the parents, unfortunately became mixed with a later sample of fledglings. However, this mixed sample, which was solitariform, did not show any marked bimodality in any morphometric character, so that the parents were most probably very similar morphometrically to the fledglings, data for which in an unmixed sample are shown in Table 2. The adults assumed to be the parents were scattered at low densities of 1·60 per mile of vehicle traverse at the time of the first observation. No swarm had been reported in this immediate area for more than 4 months previously, and even this report could not be confirmed. The coastal area for distances of over 100 miles both north and south of the site was being systematically surveyed at this time; as no swarms were observed and because of the exclusively green-extreme type of coloration of the hoppers (nymphs) at hatching (Stower 1959), it seems most probable that the parent adults were solitariform and had no recent swarming antecedents. The hopper population was large, sampling on 12 February 1950, when the fifth instar predominated, providing an estimate of 42·5 millions (95% limits ±9·3 millions in 12 sq. miles). Nevertheless, densities were low (1·14 ± 0·13 sq. yd). On the basis of hopper coloration, and except for some grouping in the first instar which apparently caused slight colour changes at this time, the hopper population was considered to be 0% congregated (Stower 1959), with mainly green-extreme colour types.

2. Zula, Eritrea (15° 15′ N, 39° 41′ E), February 1950.

This hopper population consisted of mainly green-extreme individuals which were predominantly in the fifth instar when first seen on 23 February 1950. The area was a flat, silty, flood plain and the

Table 1. *Population histories*

Statements printed across the columns refer to characteristics used for assessment in the absence of other data.

Population	Parent adults				1st Instar				Vth Instar								
	Morpho-metrics	Confi-dence	Beha-viour	Confi-dence	Density	Size and frequency of groups	Marching	Confi-dence	Density	Size and frequency of groups	Marching	Confi-dence	Time of change of behaviour	Confidence	Total confidence	Temperature and cloud	Classification of population
Akbanazuf (1)	Sol	½	D	½	L	10 Rare	0	1	L	0	0	1	0	1	4	27-31 (28) 20-24 (23) Frequently overcast	'Cool' *solitaria*
Zula (2)	Sol	½	D	½	L	Rare	0	½	L	0	0	1					
					Vth instar hopper coloration and comparison with Akbanazuf population								0 Vth coloration	½	2	X Contemporaneous with (1) Probably similar conditions	'Cool' *solitaria*
Shal Shal (3)	Sol	½	D	½	L	Rare	0	½	L	0	0	1					
					Vth instar hopper coloration and comparison with Akbanazuf population												
Dik (4)	G	¾	Sw.	1	H	Daily 500+	Daily B	1	H	Daily 500+	Daily B	1		1	4½	27.2 Cool and frequently overcast	'Cool' *gregaria*
	Other swarms in same area																
Agamat (5)	G	¾	Sw.	1	H	Daily 500+	Daily B	1	H	Daily 500+	Daily B	1	0	1	4½	29-37 (35) 16-25 (21) Frequently overcast	Modified 'Hot' *gregaria*
	Other swarms in same area																
Adarit (6)	X	½	L.Sw.	1	H	Daily 500+	Daily B	1	H	Daily 500+	Daily B	1	0	1	4½	27-35 (29) 17-24 (21) Frequently overcast	'Cool' extreme *congregans*
Khasha (7)	X	0	X	0	Hopper coloration and comparison with Ahad population												
					X	X	X	0	L	0	0	½	X	0	½	'Hot' clear skies	'Hot' extreme *dissocians* or 'Hot' *solitaria*
Beihan (8)	G	½	Sw.	½	Fledgling density and behaviour												
					X	X	X	0	L	0	0	1	1st Vth Coloration	½	2	38-43 (1946-50) Clear skies	'Hot' extreme *dissocians* or 'Hot' *solitaria*
	Parents of contemporaneous hopper bands																
Archico (9)	G	¾	Sw.	1	H	Daily 500+	Daily B & b	1	H	Daily 500+	Daily B & b	1	0	1	4¾	33-41 (37) 23-28 (26) Clear	'Hot' *gregaria*
Ailet (10)	G	1	Sw.	1	H	Daily 500+	Daily B	1	H	Daily 500+	Daily B	1	0	1	5	40-43 (41) 26-29 (28) Some cloud	'Hot' modified *gregaria*
Halibai (11)	Sol	1	D	1	L-M	10 Common 50 Rare	0	1	M	Daily 50-500	Daily D & b	1	IInd-IVth	1	5	28-32 (29) 21-25 (23) Frequently overcast	'Cool' early *congregans*
Ahad (12)	Sol	1	L.Sw.	1	L-M	50 Common Observations on similar population 70 miles distant	Daily D	¾	M	Daily 20-50	Daily D	1	P.A. Morphometrics and behaviour	½	4½	29-33 (31) Overcast at first clear later	Possibly 'Cool' *congregans*
Archico (13)	Sol+G	1	S.Sw.	1	H	Daily 500+	Daily S.B.	1	L	0	0	1	IVth	1	5	27-35 (30) 17-24 (22) Frequently overcast	'Cool' *dissocians*
Archico (14)	G	1	Sw.	1	L	0	0	1	L	0	0	1	Oviposition	1	5	28-36 (31) 17-25 (22) Frequently cloudy	'Cool' extreme *dissocians*

Morphometrics: Sol, solitariform; G, gregariform.
Behaviour, *adults*: D, low density; Sw, swarm; L. Sw, loose swarm; S. Sw, small swarm (½ sq mile).
hoppers: L, low density; M, moderate density; H, high density.

X, not known; B, large dense bands; b, small low-density bands; B & b, large dense bands breaking up into small low-density bands; D & b, low density population with local concentrations; S.B., small dense band; P.A., parent adults.

Temperature: since temperature records were not kept at Beihan at the time of the population history, the range of the daily maximum for Beihan over the period 1946-50 is given. The temperature was not recorded at Khasha but is known to be high; as it lies in the same general area as Beihan, temperatures at the same seasons could be expected to be similar. Temperatures were not recorded at Dik, but the mean maximum for Hargeisa (in the same area) for the appropriate season is given.

population was contained in a small patch of weeds (*Heliotropium* sp.), approximately 100 yd square and giving fairly uniform cover, situated at the edge of cultivations of dhurra (*Sorghum* sp.). Densities were low, not greater than 6/sq. yd. of habitat. No grouping or marching was observed. The parent adults were not seen, but the hopper coloration, and the fact that the population was contemporaneous with the one at Akbanazuf and only some 70 miles from it, suggest that the parentage might have been similar in both cases. According to hopper coloration, the population was assessed as being 0% congregated or 100% dissociated, so that even if the parents had been in swarms the hopper population had most probably existed at low densities at least since the time of hatching.

3. Shal Shal, Eritrea (15° 58′ N, 39° 12′ E), February 1950.

This population was similar in density and size to that at Zula, and in hopper colour-type composition to both the latter and the Akbanazuf populations. The locality was situated some 15 miles to the north-west of Akbanazuf; the parent adults were not observed but the proximity to the Akbanazuf population in space and time and the similarity of hopper coloration suggest that the parentage of both populations might have been similar. The habitat was a small field of dukhn (*Pennisetum typhoideum*) with extensive growth of *Heliotropium undulatum*.

4. Dik, Somaliland Protectorate (07° 45′ N, 44° 30′ E), November-December 1951.

The hoppers were in large dense bands throughout their life and were the progeny of one of a number of large dense swarms. No sample of the parent swarm was taken, but the morphometrics of other swarms in the same general area at this time were markedly gregariform. The habitat occupied by the population consisted of *Acacia–Commiphora* bush, providing a large amount of shade.

5. Agamat, Eritrea (15° 21′ N, 39° 20′ E), August-September 1953.

The hoppers of this population also were in dense bands throughout development and were the progeny of a large dense swarm. No sample of the adults was taken, but samples from nine different dense swarms observed in Eritrea at this time were closely similar morphometrically (Stower 1959). Also, two of these nine samples, taken from an area within 25 miles of Agamat (Ailet, see below) showed no significant differences between the means of the morphometric characters studied. It therefore seems reasonable to assume that the parents of the Agamat hopper population were morphometrically similar to other swarms that invaded Eritrea at this time and, like them, were markedly gregariform. The hopper bands were located in small highland valleys at an altitude of 3200 ft above sea level, amongst maize and millet crops, and were exposed to cool conditions due to the altitude and to almost continuously overcast skies.

6. Adarit, Eritrea (17° 14′ N, 38° 52′ E), February 1951.

These hoppers were in large and dense bands from hatching to fledgling, and occupied a large sandy stretch of coastal plain with extensive areas of *Panicum turgidum* and *Heliotropium pterocarpum*. The parent adults arrived as a very loose swarm of about 5 sq. miles in area; no samples were taken. At laying, intensive grouping of the ovipositing females took place.

7. Khasha, Hadhramaut (15° 45′ N, 48° 05′ E), September 1949.

A scattered population of fledglings was observed amongst fields of dhurra. Neither the hoppers nor the parent adults were observed, but the fledglings were solitariform in appearance. The population might have been from low-density or from swarming parents, but if the latter, the small numbers and low population densities of the fledglings indicate that marked dissociation had taken place.

8. Beihan, West Aden Protectorate (14° 48′ N, 45° 36′ E), August-September 1951.

A sample of fledglings was taken from an area in which there were green-extreme fifth-instar hoppers at low densities in and close to small dhurra cultivations. However, in the same general area there were hopper bands, also in the fifth-instar, but fledglings had not yet appeared amongst them. The sample of adults obtained was most probably related to the scattered hoppers, but the parentage of these was not known; they might have been derived from the same swarms that produced the hopper bands or from other populations. A sample of a swarm observed laying in this area on 24 August consisted of gregariform individuals.

9. Archico, Eritrea (15° 31′ N, 39° 28′ E), August-September 1953.

The hoppers were in large bands which were very dense during the night and also during most of the day when either moving relatively slowly or settled on vegetation; the bands tended to become less dense with very high activity during the mid-day period. The vegetation was generally sparse with some localized stands of *Acacia spirocarpa*, but consisted mainly of a poor growth of *Cenchrus ciliaris*, 3-5 cm high, and *Panicum turgidum* and *Aerva javanica* tufts along small drainage channels. The parent adults were in a large dense swarm but no sample was collected. However, the population was contemporaneous with that of Agamat (5) and Ailet (10) and the evidence suggests strongly that the parents of all these populations were gregariform and in large dense swarms (p. 315).

10. Ailet, Eritrea (15° 34′ N, 39° 10′ E), August-September 1953.

The hoppers, in large dense bands, were the progeny of gregariform adults that laid densely as a swarm. The locality was in the centre of a circular area of some 25 miles radius in which heavy breeding occurred at this time, including that observed at Agamat (5) and Archico (9). The habitat consisted largely of *Acacia* woodland which afforded an amount of shade estimated to be about 45% of the total area.

11. Halibai, Eritrea (17° 55′ N, 38° 28′ E), January-May 1949.

The parent adults were solitariform and in a low-density population. There was evidence of a gradual increase in the parent adult population with time (Stower 1959). In the first filial generation, the hopper population was very large and possibly exceeded 200 million concentrated in an area of about 8 sq. miles of *Pennisetum* cultivations. The hoppers, particularly in the later instars, formed groups, and changes of behaviour occurred which culminated in marching. The marching hoppers were not in discrete bands but formed a large moving population with a front of at least 13 miles and a depth of up to 4 miles 1 week after the first marching behaviour was observed. Within this area there was an almost continuous distribution of hoppers, with local concentrations between which the moving hoppers were at densities as low as 1 to 0·1/sq. yd.

12. Ahad, Somaliland Protectorate (09° 26′ N, 46° 48′ E), June-July 1951.

The parent adults were in very extensive but very loose swarms and were solitariform in appearance. They tended, however, to lay in dense groups, and large dense hopper bands arose from the breeding. Nevertheless, within the same area (48 sq. miles) occupied by these bands there was low-density hatching of five hoppers and less per square yard. This initially dispersed population tended to concentrate in patches of vegetation, form groups, and later marched in a very similar fashion to the hoppers observed at Halibai (11). The initially scattered hoppers were slightly older than those in dense bands and fledged first. Samples of fledglings were obtained from this part of the population but not from the dense bands. The habitat occupied by the population was a large flat sandy bed of a *tug* (seasonal watercourse) upon which were patches of low annual vegetation not exceeding 50 cm in height.

13. Archico, Eritrea (15°, 31′ N, 39° 28′ E), December-March 1950-1.

The parent adults were of both solitariform and gregariform appearance morphometrically, the population having been formed by the mixing of indigenous adults of low-density history, and immigrant adults isolated from passing swarms; the mixed scattered adults became concentrated to form a small but dense swarm (Stower 1959) which produced small hopper bands. The latter dissociated during the fourth instar, forming, together with those individuals that had been scattered since hatching, a relatively small, low-density population of highly heterogeneous history. The habitat was the same as that described for a population in this same area in a different year and season (9). Weather conditions were very cool and frequently overcast; because of low rainfall, the vegetation was sparse and of poor growth.

14. Archico, Eritrea (15° 31′ N, 39° 28′ E), December-March 1953-4.

In the same habitat as (9) and (13) but in another season, dense swarms of gregariform individuals laid at very low densities to produce hoppers which, with the exception of a few small groups which suffered high mortality and disappeared, were at low densities from the time of hatching to fledging.

In this paper, populations will be referred to by locality and by a number in parentheses which is the serial number in the above descriptions. These fourteen populations may be considered in relation to their density histories and to the environmental conditions under which the hoppers developed.

Population density may be only partially associated with the numbers of hoppers present; it is also dependent upon the effects of the structure of the habitat on the behaviour and distribution of the hoppers. Thus the biological significance of population density measured in numbers per unit area or unit volume is subject to other influences (Stower 1959) and it cannot be treated alone. For the populations described, the density histories have been assessed by consideration of one or more of the following factors:

(*a*) The volume density of hoppers within the habitat when not in groups, or marching, either at one time or at different stages in the hopper development.

(*b*) Whether or not groups of hoppers formed, either in vegetation or on the ground.

(*c*) The duration and maintenance of groups, if these were formed.

(*d*) Whether or not marching occurred and if so whether in band or loose formation.

(*e*) Hopper colour types in the fifth instar (Stower 1959).

Not all these factors were measured for each population, the extreme case being Khasha (7) where evidence was available only for the population density of the young fledglings. In all other cases, at least the coloration in the fifth instar was observed, and whether there was any group formation and marching was recorded. Hopper coloration in itself can provide evidence for the density history of a population (Stower 1959), and inferences derived from the use of this character have been given some weight in assessment of the histories of populations where long-term observations had not been possible.

The population histories to which the morphometric characters of the fledglings are to be related should ideally include data on:

(*a*) the morphometric characters of the parent adults;
(*b*) the behaviour of the parent adults;
(*c*) the density and behaviour of the filial hoppers at hatching;
(*d*) the density and behaviour of the filial hoppers in the fifth instar; and
(*e*) the time and magnitude of the changes of population density and behaviour during hopper life.

Because of the lack of uniformity in the data and the fact that the appropriate information was not obtained directly for each of these items in all cases, the population histories may be regarded as having been determinable to within five degrees of confidence depending on whether all or fewer of the foregoing conditions were known. Furthermore, each of these conditions may be treated as being known with complete certainty or by inference from other data, the latter state being ranked in $\frac{1}{4}$ degrees of confidence according to the information available. Thus the history of the Archico 1953-4 population (14) was considered as having been known with 5 degrees, and that of the Khasha (7) with $\frac{1}{2}$ degree, of confidence. This information is summarized in Table 1.

The environmental conditions to which the hoppers were exposed during development have been expressed by means of the range of maximum and minimum air temperatures at 1·5 m height and a brief statement on the general state of cloud and the type of habitat. A detailed analysis of the variation of environmental conditions would require the study of all the environmental factors, including micro-climate and the structure of the habitat. Such data were not obtained, but measurements or evidence for the temperature and cloud conditions are regarded as being the best available generalized expression of the environmental conditions, when considered together with the amount of shelter offered

by the habitat. Applying the above criteria for the determination of population density history, the populations may be classified into the following categories.

(*a*) Low-density hopper populations in which there was no evidence of an increase of density during hopper life and which probably or possibly derived from solitariform, low-density adult populations in three instances: Akbanazuf (1), Zula (2) and Shal Shal (3). In two other cases, Beihan (8) and Khasha (9), there was no completely reliable evidence of parentage, although in one instance, Beihan (8), the possibility of swarming antecedents was reasonably high. However, in this case, hopper coloration, low population density, and the absence of observed grouping suggest that even if the parents were in swarms, extreme dissociation had occurred. In the remaining population, Khasha (7), for which population history can be stated with the lowest degree of confidence, the low densities are also evidence for extreme dissociation if the parents were in swarms. All these populations were therefore of phase *solitaria* or extreme phase *dissocians* (Uvarov & Zolotarevsky 1929, Stower 1959).

(*b*) Populations of, or probably of, gregariform adults, occurring in dense swarms, producing dense hopper bands that showed no indications of dissociating at any stage. The hoppers were, in the fifth instar, fairly uniform in colour type, being either of the red-dark extreme or intermediate between the extremes and with a considerable reduction of dark pattern. Such populations may be ascribed to phase *gregaria*. Dik (4), Agamat (5), Ailet (10), Archico (9).

(*c*) Parent adults solitariform, not in swarms, but producing hopper populations, initially of green-extreme colour type, in which concentration and change of coloration and of behaviour towards those of phase *gregaria* occurred. This type of population is of early phase *congregans*. Halibai (11).

(*d*) Parent adults in extensive loose swarms and of solitariform or unknown morphometric characters, producing hoppers uniformly near the red-dark extreme colour type in dense bands that did not dissociate at any stage, and also, in one instance, Ahad (12), initially low-density hoppers which concentrated, formed groups and marched. The hoppers in bands of the two populations concerned, Adarit (6) and Ahad (12), were very closely similar in respect of the colour types present and behaviour. Both populations were also similar in that the parents were in extremely loose swarms and development of the progeny occurred in habitats of fairly low vegetation cover, with frequently overcast conditions and daily maximum temperatures within the range 27·0-34·5° C, and mean maxima of 29·4° C and 30·5° C. The evidence for the history of the parent adults at Ahad (12) prior to the first observation at this locality has been discussed by Stower (1959), and it was concluded that this large loose swarm of solitariform individuals may have originated by concentration in the adult stage of locusts that had developed in low-density populations. Because of the points of similarity in the progeny of these adults to those at Adarit, it is possible that both these populations had the same type of history of concentration in the previous generation and therefore represent a stage of phase *congregans* at a level closer to phase *gregaria* than in the case of Halibai (11). The initially scattered, but later concentrated, hoppers at Ahad were possibly intermediate in density history between those of Halibai and those in bands at both Ahad (12) and Adarit (6).

(*e*) Parent gregariform and in dense swarms, but the ensuing hoppers scattered from the time of hatching and showing changes of coloration from the red-dark towards the green extreme types. No group formation or marching occurred except amongst a small number of very small groups which suffered high mortality, the remnants dispersing in the third instar. Such a population, Archico (14), represents the extreme condition of phase *dissocians*.

(*f*) A population of highly heterogeneous history comprising both solitariform and gregariform adults from initially low-density populations and swarms, respectively, the latter having become scattered. The mixed population of two different types of adults became concentrated, forming a small but dense swarm, and oviposited in dense groups. The hoppers that were in small but dense bands were at first of a wide range of colour types, but colour changes occurred and in the fourth instar the hoppers were of, or near to, the red-dark extreme type. Dissociation then occurred and the scattered hoppers became mixed with hoppers that had been at low densities since hatching. About 50% of the adults in this population at Archico (13) were of swarming origin (Stower 1959), and although these, together with solitariform adults, formed a small swarm which bred to produce small hopper bands, the final dispersal of the latter classifieds the population as being ultimately of phase *dissocians*.

The categories of populations listed above may be further sub-divided according to the generalized statement of the environmental conditions. Two sub-classes for each category have been erected: 'cool', with mean daily maximum temperatures of about 31° C and below, and 'hot' with values of this factor of approximately 35° C or higher. In the latter sub-class, the extreme conditions are those with

high temperatures, high radiation and little shade offered by the habitat, *e.g.* Archico (9), whereas in other cases less extreme conditions were probably encountered, because of the completely overcast skies (Ailet (5)) or the shade presented by the vegetation (Ailet (10)).

ANALYSIS OF DATA

(*a*) *Historical*

Morphometrics were first used in locust studies by Uvarov (1921). He employed pairs of measurements compounded into ratios to investigate differences between the supposed species *danica* and *migratoria* in the genus *Locusta*. Uvarov showed that these were in fact extreme polymorphs, which he termed phases, of the same species, the morphometric ratios providing a measure of the differences between the extremes of a continuous range of morphological variation. He also recorded that the sexual dimorphism in size was different in the extreme phases of *L. migratoria*.

In studies on the desert locust, *Schisotcerca gregaria*, Maxwell-Darling (1934) gave a table of the morphometric data, including those for $E : F$ ratios, of seven populations showing different types of behaviour. Kennedy (1939), using the related morphometrics and behaviour of populations which he had observed, compared them with Maxwell-Darlings' table and found marked divergences from the suggested associations. Rao (1942), used a number of ratios, including $E : F$, and divided their total ranges of values into three parts characteristic of the phases *solitaria*, *transiens* and *gregaria*, respectively. Such an arbitrary division of the ranges of characters in order to define the phases offered no advantages over Maxwell-Darling's tabulated presentation. The latter method is superior, since it presents details of observed associations between morphometrics and behaviour.

Dirsh (1953) investigated a large number of body measurements and their ratios for adults of the desert locust, collected from a series of localities on different occasions, and referred to as being of phase *solitaria*, as well as for adults from swarms of phase *gregaria*. He concluded from a consideration of the means and ranges of different ratios that the best practical separation between these two extreme phases was given by the $F : C$ ratio. (The ratio of hind-femur length to vertex width ($F : V$) gave better discrimination but V was difficult to measure.) He was able to prepare a scale for measuring the 'percentage gregarization' of populations corresponding to the position of the mean $F : C$ ratios of samples within the range between the modal values for this character in his phases *solitaria* and *gregaria*. A similar scale was constructed using $E : F$ ratios but it gave less discrimination of the extreme phases. Dirsh's method allows for the dynamic nature of phase change and recognizes that although the extremes may be distinct, the intermediate stages are intergrading and cannot be divided into artificially delimited sub-ranges. A sequel to the work of Dirsh (1953) was the graphical method proposed by Rungs (1954), taking into account both $F : C$ and $E : F$ ratios, to differentiate between the phases of *S. gregaria*.

Roonwal (1949) and Roonwal & Nag (1951) set up morphometric limits for the phases *solitaria* and *gregaria* of the desert locust. They compared the measurements and the ratios of the characters *E*, *F*, *C*, *P* (length of pronotum at the keel), *H* (height of pronotum), and *M* (width of the pronotum at the constriction), as well as sexual dimorphism and eye-stripe number, made on samples taken from scattered populations in Mekran (Baluchistan) during 1935-6 and from swarms in India during the periods 1889-91 and 1930-1. There was no recorded evidence for the population histories before sampling. Misra, Nair & Roonwal (1952) using *E*, *F*, *C* and *P*, applied the method of discriminant function analysis to differentiate the phase status of various populations. The characters *F*, *C* and *P* were all found to discriminate, but in varying degrees, *C* being the best. In the case of females, *F* also was a reliable discriminant. Nair pointed out in this paper that the sample of phase *gregaria* was possibly heterogeneous because the adults were collected from different localities in different seasons.

Albrecht & Blackith (1957) and Blackith (1957) used a modification of a method of analysis related to that employed by Misra, Nair & Roonwal (1952) in order to study phase status in *Nomadacris septemfasciata* (Serv.) and *Schistocerca gregaria* and also polymorphism in some Australian Acrididae. The form of multivariant analysis employed by Albrecht & Blackith (1957), and used in this paper, has distinct advantages over the previous single-character and ratio comparisons in that it makes much fuller use of all the morphometric data, is more sensitive, and can provide a concise geometrical presentation of the relationships of morphometrics with various recorded environmental factors.

In general, emphasis has been placed upon the discrimination of phase, or density-dependent, characters through the morphometrics. Consideration does not appear to have been given to the effects upon morphometric phase characters of factors unrelated to density, particularly those associated with the environmental conditions during development. Exceptions to this are the observations of Zolotarevsky & Murat (1938) of higher $E : F$ ratios in scattered adults from dry areas than in those from more humid ones; the report by Husain & Mathur (1944) that isolated hoppers reared in the laboratory at 27° C gave adults with larger measurements and lower $E : F$ ratios than those bred at 40° C; the observation by Adamović (1950) that individuals of *Oedipoda coerulescens* (L.) from localities at 1500 m above sea level were smaller than those from 120 m, and the studies of Brett (1947) on *Melanoplus m. mexicanus* (Saussure) in which individuals reared in the laboratory on a stabilized diet were larger in respect of *E*, *F* and *C* when developing at 38° C than at 24° C. It appears possible, therefore, that environmental factors such as temperature and humidity may affect the morphometrics in Acrididae, and that in a swarming species such as *Schistocerca gregaria* this variation may produce effects resembling those associated with density.

An important aspect of phase variation which has been given some attention in relation to the way in which it can be discerned by means of morphometrics, is that of the direction of change, or whether a population may be assigned to phase *congregans* or to phase *dissocians*. Roonwal (1945) and Misra, Nair & Roonwal

(1952) have considered this aspect, particularly in relation to the percentage of individuals with six or with seven eye-stripes, and to the sex ratio in a population. No conclusive evidence, however, has been published showing the possibility of discriminating between phases *congregans* and *dissocians* on the basis of morphometrics, although Albrecht & Blackith (1957), using principally the shape of the wing pads of hoppers of *Nomadacris septemfasciata*, and Stower (1959), employing measurements of the colour patterns of the hoppers of *Schistocerca gregaria*, have provided evidence for the possibility of differentiating between these phases in the nymphal stages.

(*b*) *Multivariant analysis in relation to the populations studied*

The relative merits of the ratio and the discriminant function methods of morphometric analysis have been discussed by Blackith (1957). Discrimination of the effects of different intensities of any given factor upon the appropriate morphological characters of insects may be achieved by expressing the difference of the arithmetic means of samples of these characters as multiples of their residual variability. These multiples of character differences, used either as univariants or multivariants, can be employed for the '*t*' test or variance ratio (*F**)* estimations of their statistical significance. A ratio, in effect, is a univariant, and the interrelationship of the pairs of characters is hidden in the residual variability, making the latter a less sensitive comparison unit than the residual variability of pairs of characters used as multivariants. The immediate apparent advantage of ratios is that they are independent of individual size, but the latter in itself may be of importance when considering the morphological expressions of reactions to the environment. Discriminant functions are not only more sensitive measures of morphological differences than ratios, because of the multivariant form of analysis, but they are also vectors which define the direction and degree in which groups of characters differ. Because of this characteristic, they may be used to distinguish the effects upon morphometrics of density-dependent and density-independent factors. The effects of different environmental conditions upon morphometrics may be illustrated by three-dimensional or projected diagrams (Albrecht & Blackith 1957, Blackith 1957) in which the characteristics associated with, for example, species may be in a plane different from that of, for example, phase. In the present studies, where there has been a broad classification of the populations into density history (density dependence) and into generally 'cool' or 'hot' environmental conditions for development (density independence), the effects of both sets of factors upon the morphometrics, expressed by discriminant function analysis, did in fact lie in the same plane (p. 324).

In the present investigations, *E*, *F* and *C* measurements in millimetres were available for both sexes, giving sixteen sub-samples (Khasha & Beihan being combined) of the morphometrics of a total of 849 adult desert locusts for the analysis, together with the arithmetic means of *E*, *F* and *C* for both sexes of

* *F** replaces *F* as used in standard statistical formulae concerning variance ratio significance tests, since *F* is used elsewhere in the text to represent the length of hind femur.

Table 2. *The morphometric characters for fourteen populations of the desert locust*

E, *F* and *C* only, for both sexes, have been used for the analysis; *E*:*F* and *F*:*C* ratios are shown for reference purposes only.

		Male				Female				*E*:*F*		*F*:*C*	
		n	*E*	*F*	*C*	*n*	*E*	*F*	*C*	male	female	male	female
Dik**	(4)	33	52·267	23·703	7·488	36	57·500	25·522	7·939	2·20	2·25	3·16	3·21
Adarit	(6)	110	53·484	24·765	7·503	112	60·250	27·214	8·146	2·16	2·22	3·30	3·34
Agamat	(5)	90	51·660	23·167	7·152	93	55·809	25·243	7·711	2·20	2·24	3·20	3·25
Zula	(2)	18	50·833	25·083	6·517	10	60·440	29·330	7·640	2·03	2·06	3·86	3·84
Shal Shal	(3)	13	48·908	24·308	6·423	12	60·592	29·942	7·725	2·02	2·03	3·78	3·87
Akbanazuf**	(1)	43	49·877	24·635	6·405	38	61·292	30·287	7·868	2·03	2·03	3·93	4·01
Khasha*	(7)	17	51·071	25·512	6·529	9	60·722	30·578	7·433	2·04	2·06	3·86	3·96
Beihan	(8)									1·96	1·97	3·97	4·16
Archico*	(9)	108	51·617	25·464	6·642	107	60·243	29·277	7·460	2·03	2·06	3·83	3·94
Ahad Tug Parents	(12)	11	53·436	26·273	6·900	16	63·606	30·925	7·931	2·04	2·06	3·82	3·89
Ahad Tug F_1		38	56·158	26·724	7·195	25	64·300	30·536	8·084	2·11	2·11	3·72	3·78
Archico Parents	(14)	195	52·858	23·894	7·611	126	58·866	25·952	8·148	2·22	2·26	3·15	3·21
Archico F_1		37	50·210	24·850	6·714	27	60·260	29·260	7·800	2·02	2·06	3·69	3·75
Archico Sample D_2	(13)	34	48·160	22·980	6·494	19	54·240	25·400	7·253	2·10	2·14	3·54	3·50
Archico Sample D_3		34	46·390	22·350	6·344	16	52·080	24·600	6·963	2·10	2·16	3·46	3·46
Ailet	(10)	99	49·042	23·272	6·692	62	56·113	26·252	7·348	2·11	2·14	3·51	3·58
Halibai Parents	(11)	28	50·018	24·211	6·182	22	60·941	29·723	7·400	2·07	2·05	3·96	4·04
Halibai F_1		22	53·530	25·720	6·864	17	61·880	29·740	7·729	2·08	2·08	3·75	3·84

** Reference subsamples 'cool'.
* Reference subsamples 'hot'.
n = number of locusts.

parent and first filial generations, for nine further cases and eighteen further sub-samples (Table 2). The samples were taken from the fourteen populations listed in Table 1 that had developed under a wide range of density and 'temperature' conditions. These data were used for the calculation of the error matrix of variances and co-variances.

The following preliminary calculations were made for the analysis: sub-sample totals, arithmetic means and correction terms of the type ΣE, $\bar{e}$, $(\Sigma E)^2/n$ and (ΣE) $(\Sigma F)/n$, as well as the grand totals of characters, of squares of characters and of products of characters, and grand correction terms of the type ΣE, ΣE^2, ΣEF, $(\Sigma E)^2/N$, and (ΣE) $(\Sigma F)/N$ where Σ = the sum of, n = number of insects in sub-sample, and N — grand total of insects. The sub-sample arithmetic means are listed, together with the sub-sample numbers, in Table 2, and the 'sums of squares' and 'sums of products' for the total and the sub-samples, derived from subtractions of the type $\Sigma E^2 - (\Sigma E)^2/N$ and $\Sigma EF - (\Sigma E)$ $(\Sigma F)/N$, are recorded in Table 3, where the 'error sums of squares' and products are obtained by subtracting the appropriate sub-sample entry from the total entry. The residual variability is obtained by dividing the error entries by the error degrees of freedom. These

Table 3. *Analysis of variances and covariances*

Item	d.f.	Σe^2	Σf^2	Σc^2	Σef	Σfc	Σec
Total	848	16591·79	5309·30	353·39	7206·88	519·13	1710·36
Sub-samples	15	13555·93	3788·40	243·18	6132·78	381·42	1452·01
Error	833	3035·86	1520·90	110·21	1074·10	137·71	258·35
Residual variability		3·6444898	1·8258103	0·13230492	1·2894358	0·16531813	0·31014406

elements of the residual variability are error mean squares and mean covariances and must then be arranged in a square matrix. Differences of appropriate arithmetic means of characters of sub-samples to be compared, can then be divided by this matrix. This division is affected by multiplying these differences by the inverse of the error, or dispersion matrix. Linear equations are obtained, which, algebraically combined, give Mahalanobis's generalized distance (D^2) (Mahalanobis 1936) which, square-rooted as used by Rao (1952) and extended in form of application by Blackith (1957), can provide interpretative diagrams of the positions of the sub-samples in relation to the effects considered. These calculations result in single measures, compounded from several morphometric differences of various populations, in terms of a unit analogous to a 't' value. The form of compounding these single measures of population differences, corresponds to the differing effects on the various morphometrics considered, by either sex or measured environmental factors. In the construction of an interpretative diagram any of the above single measures of population differences can be used as a base line because they correspond to the relevant factors in magnitude and direction.

Matrices can be inverted by the pivotal-condensation method (Aitken 1933) as used and modified by Rao (1952) or, as adopted here, by the Cholesky technique as outlined in Skan (1954) and described and illustrated by a worked example

below. A typical generalized distance (D^2) between two sub-samples follows, together with a variance ratio significance test. It should be noted that appropriate sets of sub-sample arithmetic means in Table 2 provide reference points from which arithmetic means of the same characters in a sub-sample to be investigated can be subtracted. The resulting differences can then be multiplied by the inverted dispersion matrix, calculated in this section, to give generalized distances which can serve to place that sub-sample in its density-dependent and density-independent size dimensions relative to the reference sub-samples of known history.

A matrix (X) can be expressed in the form $(X) = LL'$ where L is a lower triangular matrix and L' is its transpose. Similarly, the inverse of (X), *i.e.* $(X)^{-1} = L^{-1}(L^{-1})'$. The lower triangular matrix designated (x) is derived from the dispersion matrix (X). This triangular matrix is inverted and the inversion multiplied by its transpose (y) to give the inverted dispersion matrix designated (Z).

Dispersion matrix (X):

$$\begin{matrix} X_{11} & X_{12} & X_{13} \\ X_{21} & X_{22} & X_{23} \\ X_{31} & X_{32} & X_{33} \end{matrix}$$

Lower triangular matrix (x):

$$x^2_{nn} = X_{nn} - \sum_{p=1}^{p=n-1} x^2_{np};$$

$$x_{mn} = \left\{ X_{mn} - \sum_{p=1}^{p=n-1} x_{mp}x_{np} \right\} / x_{nn}$$

$$x_{11} = \sqrt{X_{11}}$$

$$x_{21} = X_{21}/x_{11} \qquad x_{22} = \sqrt{X_{22} - x^2_{21}}$$

$$x_{31} = X_{31}/x_{11} \qquad x_{32} = (X_{32} - x_{21}x_{31})/x_{22} \qquad x_{33} = \sqrt{X_{33} - (x^2_{31} + x^2_{32})}$$

Inverted transposed triangular matrix (y):

$$y_{nn} = 1/x_{nn}; \; y_{mn} = -\left\{ \sum_{p=m}^{p=n-1} x_{np}y_{mp} \right\} / x_{nn}$$

$$y_{11} = 1/x_{11} \qquad y_{12} = -(x_{21}y_{11})/x_{22} \qquad y_{13} = -(x_{31}y_{11} + x_{32}y_{12})/x_{33}$$

$$y_{22} = 1/x_{22} \qquad y_{23} = -(x_{32}y_{22})/x_{33}$$

$$y_{33} = 1/x_{33}$$

Inverted dispersion matrix (Z):

$$Z_{nn} = \sum_{p=n}^{p=r} y^2_{np}; \qquad Z_{mn} \sum_{p=n}^{p=r} y_{mp}y_{np}$$

$$Z_{11} = y^2_{11} + y^2_{12} + y^2_{13} \qquad Z_{12} = y_{22}y_{12} + y_{23}y_{13} \qquad Z_{13} = y_{33}y_{13}$$

$$Z_{21} = Z_{12} \qquad Z_{22} = y^2_{22} + y^2_{23} \qquad Z_{23} = y_{33}y_{23}$$

$$Z_{31} = Z_{13} \qquad Z_{32} = Z_{23} \qquad Z_{33} = y^2_{33}$$

where r = order of matrix

viz., 3×3 matrix; $p = r = 3$

Dispersion matrix (X):

$X_{11} = 3{\cdot}6444898$	$X_{12} = 1{\cdot}2894358$	$X_{13} = 0{\cdot}31014406$
$X_{21} = 1{\cdot}2894358$	$X_{22} = 1{\cdot}8258103$	$X_{23} = 0{\cdot}16531813$
$X_{31} = 0{\cdot}31014406$	$X_{32} = 0{\cdot}16531813$	$X_{33} = 0{\cdot}13230492$

Lower triangular matrix (x):

$x_{11} = 1{\cdot}9090547$		
$x_{21} = 0{\cdot}67543157$	$x_{22} = 1{\cdot}1703002$	
$x_{31} = 0{\cdot}16245949$	$x_{32} = 0{\cdot}047498806$	$x_{33} = 0{\cdot}32195605$

Inverted transposed triangular matrix (y):

$y_{11} = 0{\cdot}52381946$	$y_{12} = -0{\cdot}30231918$	$y_{13} = -0{\cdot}21971832$
	$y_{22} = 0{\cdot}85448163$	$y_{23} = -0{\cdot}12606335$
		$y_{33} = 3{\cdot}1060140$

Inverted dispersion matrix (Z) used with differences of means to calculate generalized distances (D^2):

$Z_{11} = 0{\cdot}41405985$	$Z_{12} = -0{\cdot}23062776$	$Z_{13} = -0{\cdot}68244818$
$Z_{21} = -0{\cdot}23062776$	$Z_{22} = 0{\cdot}74603082$	$Z_{23} = -0{\cdot}39155453$
$Z_{31} = -0{\cdot}68244818$	$Z_{32} = -0{\cdot}39155453$	$Z_{33} = 9{\cdot}64732297$
Check: 0·99999996	*1·00000000*	*0·99999998*

It should be noted that measurements are made to a maximum of three figures and since the above entries in the matrices can be considered as squares and cross multiples at least six figures must be carried and preferably two extra to counteract rounding-off errors in the sixth figure which occur with continued multiplication and addition. The accuracy of the inverted dispersion matrix may be checked by summing the multiples of corresponding elements of both inverted matrix and the original dispersion matrix, either in each row or in each column, and equating to unity. Divergence from unity may be accepted in the seventh figure but should occur preferably not higher than the eighth. Confidence in the sixth figure of the inverted matrix is then assured and hence in the third figure of the derived 'D' values. The check equation type is as follows:

$$X_{11}Z_{11}+X_{21}Z_{21}+X_{31}Z_{31} = 1{\cdot}00000000$$

THE MORPHOMETRIC LIMITS FOR PHASES *SOLITARIA* AND *GREGARIA*

The Akbanazuf population (1) was selected as being one of which the parents probably had no immediate swarming antecedents and the resulting hoppers developed at low densities, showing hardly any signs of grouping and no marching (phase *solitaria*). At the other extreme of density history, where the parents were in swarms and the resultant hoppers were in large bands throughout their life-histories, the Dik population (4) has been selected as being typical of phase *gregaria*. Both populations developed under 'cool' conditions so that the effects of differences of temperature have been minimized.

(*a*) *The generalized distance between 'cool'* gregaria *male and 'cool'* solitaria *male sub-samples*

The arithmetic means of the characters E, F and C of the two sub-samples selected are subtracted in Table 4 to give differences of the type 'e' $= (\bar{e}_1 - \bar{e}_2)$. These differences are multiplied by their corresponding inverted dispersion matrix

Table 4. *Calculation of differences*

	E	F	C
'Cool' *gregaria* males	52·267	23·703	7·488
'Cool' *solitaria* males	49·877	24·635	6·405
Difference	+2·390 (e)	−0·932 (f)	+1·083 (c)

elements and summed in the rows in turn to give the coefficients β_1, β_2 and β_3. The sum of multiples of these coefficients and the corresponding mean differences give the value of the generalized distance (D^2) as in the equation:

$$D^2 = \beta_1 . e + \beta_2 . f + \beta_3 . c$$

The calculation of the coefficients is formulated below and illustrated by entries from Table 4 and the inverted dispersion matrix.

$$\beta_1 = eZ_{11} + fZ_{12} + cZ_{13}$$
$$\beta_2 = eZ_{21} + fZ_{22} + cZ_{23}$$
$$\beta_3 = eZ_{31} + fZ_{32} + cZ_{23}$$

$$\beta_1 = (2{\cdot}39)(0{\cdot}41405985) + (-0{\cdot}932)(-0{\cdot}23062776) + (1{\cdot}083)(-0{\cdot}68244818)$$
$$\beta_2 = (2{\cdot}39)(-0{\cdot}23062776) + (-0{\cdot}932)(0{\cdot}74603082) + (1{\cdot}083)(-0{\cdot}39155453)$$
$$\beta_3 = (2{\cdot}39)(-0{\cdot}68244818) + (-0{\cdot}932)(-0{\cdot}39155453) + (1{\cdot}083)(9{\cdot}64732297)$$

Whence $\beta_1 = +0{\cdot}46545673$; $\beta_2 = -1{\cdot}67055463$; $\beta_3 = 9{\cdot}18192845$

and $D^2 = (2{\cdot}39)(0{\cdot}46545673) + (-0{\cdot}932)(-1{\cdot}67055463) + (1{\cdot}083)(9{\cdot}18192845)$
$= 12{\cdot}61342694$

and $D = 3{\cdot}552$

The significance of such discriminants can be obtained from the variance ratio, F^*, calculated below:

$$F^* = \frac{n_1 n_2 (n_1 + n_2 - 1 - p) D^2}{p(n_1 + n_2)(n_1 + n_2 - 2)};$$

for degrees of freedom (d.f.) $= p$, $(n_1 + n_2 - 1 - p)$

where p = number of characters used in analysis
n_1 = number of insects in the first sub-sample
n_2 = number of insects in the second sub-sample

$$F^* = \frac{(43 \times 33)(43 + 33 - 1 - 3)(12{\cdot}61342694)}{3(43 + 33)(43 + 33 - 2)}$$
$$= 76{\cdot}380;\ \text{d.f.} = 3,\ (43 + 33 - 4);\ \text{probability}\ (P) < 0{\cdot}001$$

i.e. the discriminant estimated above is highly significantly different from zero.

The above analytical methods, when extended to the remaining sub-samples of the 'cool' *gregaria* (Dik (4)) and 'cool' *solitaria* (Akbanazuf (1)) collections, provided a total of six significant generalized distances. The square roots of these values are entered in Table 5. It should be noted that the biggest contributor to the male phase discriminant is the '*c*' value, corresponding to the character *C*. This is in contrast with the female phase discriminant where the '*f*' value corresponding to the *F* character is the dominant contributor. In both the high and low density sex discriminants the character *E* is of most importance, whilst in the high-density male/low-density female and the high-density female/low-density male discriminants, the pairs of characters *E* and *F*, and *E* and *C* are respectively

Table 5. *Comparison of 'cool' sub-samples*

Sub-sample comparisons	'*D*' values	d.f.	Variance ratios	Probability
'Cool' *gregaria* male-'Cool' *solitaria* male	$D_1 = 3{\cdot}552$	3; 72	76·380	$P<0{\cdot}001$
'Cool' *gregaria* female-'Cool' *solitaria* female	$D_2 = 3{\cdot}904$	3; 70	91·299	$P<0.001$
'Cool' *gregaria* male-'Cool' *gregaria* female	$D_3 = 2{\cdot}741$	3; 65	41·843	$P<0{\cdot}001$
'Cool' *solitaria* male-'Cool' *solitaria* female	$D_4 = 6{\cdot}277$	3; 77	258·264	$P<0{\cdot}001$
'Cool' *solitaria* male-'Cool' *gregaria* female	$D_5 = 5{\cdot}222$	3; 75	173·510	$P<0{\cdot}001$
'Cool' *solitaria* female-'Cool' *gregaria* male	$D_6 = 5{\cdot}780$	3; 67	190·990	$P<0{\cdot}001$

of equal importance for differentiation. The full comparative analysis thus demands the use of all three morphometric characters.

(b) The construction and interpretation of simple and compound 'D' diagrams

Interpretation of the observed effects of environmental factors on measured morphological characters may be achieved by inspection of simple or compound discriminant diagrams, constructed from estimates of the generalized distances between the various sub-samples subjected to the observed environmental conditions. The construction and interpretation of a simple diagram, in which two extreme conditions of one environmental factor were observed, are described below. It should be noted that, given three characters, a discriminant diagram having four apices can have three dimensions, thus forming some kind of tetrahedron. Two of these dimensions could be identified with size and density factors and the third identified with high sample variation or an unknown or unmeasured factor. Two heterogeneous samples gave tetrahedra, but where it was possible to break one sample down into homogeneous components these gave two-dimensional stable diagrams as did all the other homogeneous samples analysed in this paper. Effectively the two dimensions are at right angles, one corresponding to density or temperature effects on morphometrics, the other to effects largely independent of density or temperature.

The effect of the single factor of density, free of other known and unknown factors, on the three measured characters, *E*, *F* and *C*, of locusts in the 'cool' *gregaria* and 'cool' *solitaria* collections, is illustrated in the simple discriminant diagram (Fig. 1) which is based on the '*D*' values entered in Table 5. The figure

is commenced by choosing one of the '*D*'s, 'cool' *solitaria* male to 'cool' *solitaria* female (D_4), as the base line. One end of this base is the position of the male sub-sample, the other that of the female sub-sample. The position of the 'cool' *gregaria* female is found by using the 'cool' *solitaria* male end as centre and the discriminant D_5 as radius, and the 'cool' *solitaria* female as centre and D_2 as radius to complete the triangle. The remaining position, 'cool' *gregaria* male, is obtained by radii D_3 from the 'cool' *gregaria* female position and D_1 from the 'cool' *solitaria* male position. The remaining diagonal discriminant D_6 should and does fit this diagram. Where this latter condition is fulfilled, the resulting two-dimensional structure can be described as stable. Further analyses have shown that similar stable two-dimensional diagrams, corresponding to other pairs of comparisons, may be fitted to this diagram. Check diagonal discriminants in the stable diagrams were found to have errors in length much less than 5% and generally less than 1%.

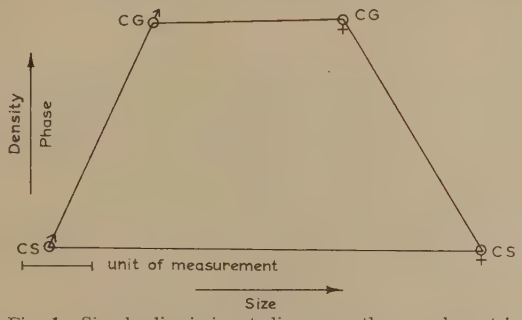

Fig. 1. Simple discriminant diagrams: the morphometric limits for phases *solitaria* and *gregaria* under 'cool' conditions.
CS = 'Cool' *solitaria*, Akbanazuf (1)
CG = 'Cool' *gregaria*, Dik (4)

These errors consist in part of errors of analysis, draughting error, non-linearity of character interrelations and frequency distribution disturbances.

Tetrahedral diagrams were obtained from the estimated discriminants of two sets of samples, one a laboratory sample and the other a field sample from Agamat (5). The laboratory sample, used for experimental purposes (Norris 1952), was known to consist of three stocks of different origin. Detailed examination of the raw morphometric data, using a graphical, polymodal, frequency-distribution, analytical method (Harding 1949), gave three populations from the caput width (*C*) measurements. These populations corresponded very closely to the three stocks. A discriminant analysis using one stock ('Old Stock') gave a stable two-dimensional diagram. Similar graphical analysis of the Agamat sample apparently showed heterogeneous populations of caput measurements. Further inspection of the raw data revealed an undue preponderance of the round figure 7·0 mm, which suggested that the sample's heterogeneity in distribution of caput width was due to faulty measurement.

The limits given here for phases *solitaria* and *gregaria* under 'cool' conditions,

as under all other sets of conditions described later, are those found in the data obtained and may possibly be exceeded with examination of further data. However, they may be regarded as being representative of the limits that might be expected. In Fig. 1, the size dimension in respect of *E*, *F* and *C* is from left (small) to right (large) of the diagram and the phase dimension from bottom (*solitaria*) to top (*gregaria*). It may be seen that factors affecting size (such as possibly the amount of available food) might displace the diagram to the left (smaller) or to the right (larger). Also there is a size difference between the sexes, the males being smaller, but the sexual dimorphism is greater in *solitaria* than in *gregaria*. Hence the relative size between the sexes varies along the phase dimension and the density-dependent factors must influence size differentially in the sexes. The sex dimension can therefore be regarded as being in general one of size, but since it changes with density it cannot be purely related to size (Blackith 1957); if it were so related Fig. 2 would be a parallelogram.

(*c*) *The morphometric limits for phases* solitaria *and* gregaria *under 'hot' conditions*

It cannot be stated with confidence that the samples obtained at Khasha (7) and Beihan (8) were from populations that had no immediate swarming history. Indeed, in the former case there is a reasonably strong possibility that the parents were in swarms. However, the low population densities, the absence of grouping, and the hopper coloration at Beihan indicated that they had been at low densities for the greater part of their life as hoppers. Consequently, these populations may have been of phase *dissocians* and therefore do not provide data for the limits of morphometric characters for phase *solitaria* under 'hot' environmental conditions. This does not preclude regarding their morphometrics as approaching those of phase *solitaria* under 'hot' conditions, and the comparisons of the morphometric data with those of populations of different types of histories is of interest. The morphometric data for the Khasha and Beihan fledgling samples have been combined. The Archico (9) sample has been taken as being representative of phase *gregaria* under 'hot' conditions.

The simple generalized-distance diagram for the morphometrics of populations of phases *solitaria* and *gregaria* under 'hot' conditions constructed in the manner already described has been compounded with that for the two extreme phases under 'cool' conditions (Fig. 1) and is shown as Fig. 2. To relate the two simple diagrams for 'cool' and 'hot' conditions, six extra discriminant functions, chosen for giving clear intersecting arcs, were used, together with two of the *D*'s, for the 'hot' conditions (Table 6). The latter *D*'s were used as the base line of that section of the compound diagram pertaining to the 'hot' conditions and the remaining six values for '*D*' shown in Table 6 were employed in checking the stability of the diagram. The apices of the simple diagram for a 'cool' environment are used as the basic reference points from which the appropriate *D*'s are drawn to fix the relative positions of apices of the simple diagram for the 'hot' environment. It should be noted that the discriminant D_8 ('hot' *solitaria* male-'hot' *gregaria* male;

Table 6) is non-significant, but the validity of the relative positions of the 'hot' solitary males and 'hot' gregarious males is established both by remaining significant discriminants and by the stability of the whole diagram as well as its components. This is a further advantage of this particular use of multivariants over that of univariants such as ratios.

Table 6. *'D' values for 'hot' and 'cool' conditions*

Sub-sample comparisons	'D' values	d.f.	Variance ratios	Probability
'Cool' *gregaria* male-'Hot' *solitaria* female	D_1 6·245	3; 38	87·342	P<0·001
'Cool' *gregaria* female-'Hot' *solitaria* male	D_2 4·886	3; 49	88·286	P<0·001
'Cool' *solitaria* male-'Hot' *solitaria* female	D_3 5·963	3; 48	84·688	P<0·001
'Cool' *solitaria* female-'Hot' *solitaria* male	D_4 5·600	3; 51	118·15	P<0·001
'Cool' *solitaria* male-'Hot' *gregaria* female	D_5 5·507	3;146	305·87	P<0·001
'Cool' *solitaria* female-'Hot' *gregaria* male	D_6 5·317	3;142	261·22	P<0·001
'Hot' *solitaria* female-'Hot' *gregaria* female	D_7 1·176	3;112	3·757	P<0·025
'Hot' *solitaria* male-'Hot' *gregaria* male	D_8 0·509	3;121	1·247	P>0·250

'Hot' *gregaria* = Archico (9).
'Hot' *solitaria* = Khasha (7) and Beihan (8).

The relative positions of the two simple diagrams within the compound stable figure (Fig. 2) indicate that the temperature effect on morphometrics acts in a dimension that is not only parallel to the density-dependent (phase) dimension but is in the same plane, formed by the size and phase dimensions. Furthermore,

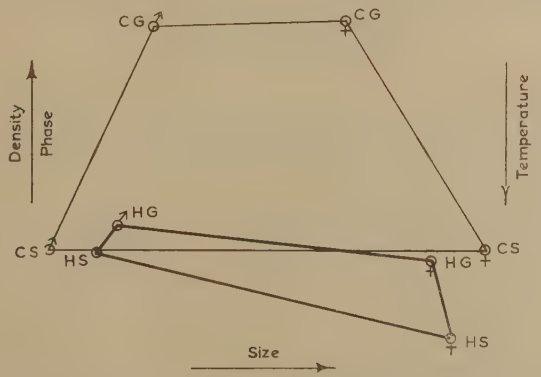

Fig. 2. Compound discriminant diagram: the morphometric limits for 'cool' and 'hot' *solitaria* and *gregaria*.
HS = 'Hot' *solitaria*, Khasha (7) and Beihan (8)
HG = 'Hot' *gregaria*, Archico (9)
(Other symbols as in Fig. 1)

the morphometric characters of phase *gregaria* from a 'hot' developmental environment are similar in some respects to those of phase *solitaria* from a 'cool' developmental environment, as is shown by the close proximity of the respective lines representing the two types of population. The morphometric characteristics of phase *solitaria*, or of phase *dissocians* approaching the latter status, under 'hot'

conditions of development are displaced, relative to the data for 'cool' environments, to a more extreme *solitaria* position along the phase dimension. The sexual dimorphism for phase *gregaria* from 'hot' developmental conditions is relatively lower than for populations approaching phase *solitaria* under similar conditions, but it is also lower than for individuals of phase *solitaria* that have existed as hoppers under 'cool' conditions. It may be, therefore, that sexual dimorphism is a character of possible use in discriminating between populations of the same general morphometric characters but of different phases from different types of environment. Differences of environmental conditions indicated by the general order of temperatures recorded may therefore affect morphometrics in a way that is

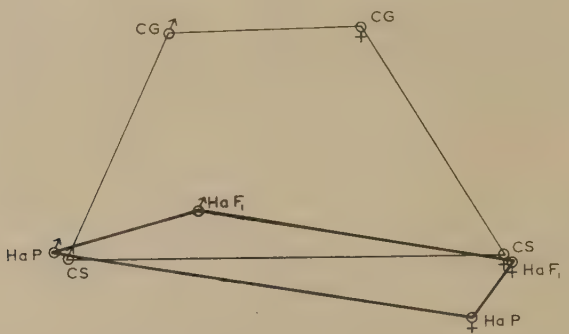

Fig. 3. *Congregans* population in relation to parental morphometrics and the limits for *solitaria* and *gregaria*.
Ha.P = Halibai (11) parents
Ha.F_1 = Halibai (11) progeny

expressed as changes in the same plane of the generalized distance diagram as for density-dependent factors, but in a direction opposite to them.

(*d*) *The relationships of the morphometrics of other populations to the limits for phases* solitaria *and* gregaria *under 'cool' and 'hot' conditions*

The phase status of populations with histories known with a greater or lesser degree of confidence (pp. 311-4, Table 1) may now be considered in relation to the approximate morphometric limits for *E*, *F* and *C* of phases *solitaria* and *gregaria*.

The stable discriminant function diagram for the phase *congregans* population (Halibai (11)), in which concentration and congregation occurred in the hopper stages, is shown in relation to the limits for phases *solitaria* and *gregaria* in Fig. 3, the appropriate *D* values being given in Table 7. The morphometric data for the parent adults fall very close to those for 'hot' *gregaria* and 'cool' and 'hot' *solitaria*, but are closest to the latter (*cf.* Fig. 2). However, in respect of sexual dimorphism, indicated by the length of the horizontal line, the population approached more closely the 'cool' *solitaria*. In terms of the morphometric characters used the parent adults at Halibai (11) were therefore possibly of phase *solitaria*, and not *gregaria* that had developed under hot conditions which, morphometrically, show

some resemblances to *solitaria*. Evidence from the eye stripes (p. 333) supports this conclusion and Stower (*in preparation*) concludes that these parent adults arose from an early winter generation on the Eritrean coast, *i.e.* they were 'cool' *solitaria*. Consequently the reference points for 'cool' *solitaria* given by the Akbanazuf (1) sample were possibly not fully representative of the extreme limit for this status. The morphometric characters of the ensuing fledglings at Halibai (11) show a shift, relative to the parents, along the phase dimension towards phase *gregaria*. The magnitude of the shift compared with that possible between the suggested limits for the phases was small, and morphometrically these adults

Table 7. *'D' values for the population Halibai (11)*

	'D' values	d.f.	Variance ratios	Probability
'Cool' *gregaria* male-Halibai P female	5·970	3;51	150·88	P<0·001
'Cool' *gregaria* female-Halibai P male	5·475	3;60	152·28	P<0·001
'Cool' *solitaria* male-Halibai P female	5·882	3;61	162·50	P<0·001
'Cool' *solitaria* female-Halibai P male	6·483	3;62	218·81	P<0·001
'Cool' *solitaria* male-Halibai F_1 female	6·384	3;56	159·83	P<0·001
'Cool' *solitaria* female-Halibai F_1 male	4·433	3;56	88·130	P<0·001
Halibai P male-Halibai F_1 male	2·185	3;46	18·786	P<0·001
Halibai P female-Halibai F_1 female	0·988	3;35	2·952	P<0·05
Halibai F_1 male-Halibai F_1 female	4·481	3;35	60·716	P<0·001
Halibai P male-Halibai P female	5·932	3;46	138·5	P<0·001
Halibai P male-Halibai F_1 female	6·493	3;41	141·7	P<0·001
Halibai F_1 male-Halibai P female	4·084	3;40	58·254	P<0·001

Halibai P = Halibai parent generation.
Halibai F_1 = Halibai F_1 generation.

were only slightly different from 'cool' *solitaria* but differed in the relatively larger size of the males with a correspondingly smaller sexual dimorphism.

For the Ahad (12) parent population, the calculated position representing it in the generalized distance diagram coincides with a position intermediate between that for 'cool' *solitaria* and the F_1 Halibai (11) population (Fig. 4; Table 8). On the criteria used it may therefore be suggested that this population developed under 'cool' conditions and was possibly *solitaria* or early *congregans*; it differs from the characteristics of the extreme 'hot' *gregaria* (Fig. 2) in the larger size of the individuals and a larger sexual dimorphism. Stower (1959*f*...4) discussed the possible history of this population and considered that it was most likely to have arisen from low-density hopper populations under 'cool' environmental conditions and that its history was related to the early stages of congregation. The fledglings arising from breeding by these adults showed, morphometrically, a shift along the phase dimension of the same sort of magnitude as for Halibai (11) (Fig. 3). These fledglings arose from hoppers that were initially scattered but which later concentrated to form loose, marching groups. No samples of fledglings from the part of this population that was in dense hopper bands throughout development were obtained. However, evidence for the similarities of history between these

bands and those at Adarit (6) has been given (p. 315). The morphometric characters of the young adults of the latter population (Fig. 4; Table 8) approach more closely the limits for phase *gregaria* of 'cool' developmental history.

In the Archico (14) population which dissociated in a 'cool' environment (Fig. 5; Table 8), the parents coincided morphometrically in the stable generalized distance

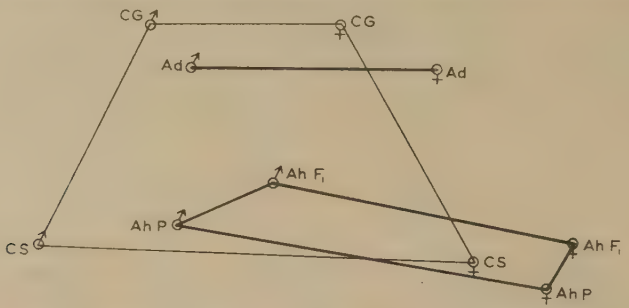

Fig. 4. *Congregans* population in relation to parental morphometrics and the limits for *solitaria* and *gregaria*.
Ah.P = Ahad Tug (12) parents
Ah.F_1 = Ahad Tug (12) progeny
Ad = Adarit (6)

diagram with 'cool' environment phase *gregaria*, but the fledglings were morphometrically very close to 'cool' phase *solitaria*. Hence, the shift along the phase dimension was almost the maximum that might be envisaged as occurring under these conditions.

The discriminant of the fledglings at Ailet (10), which were of phase *gregaria* developing in a 'hot' but shaded environment, showed a shift along the phase

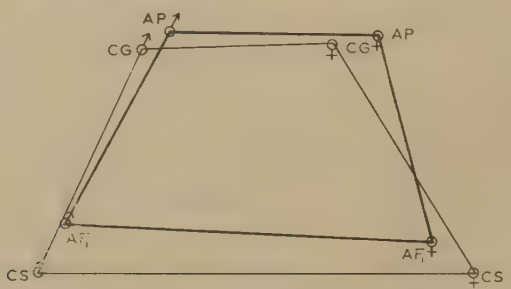

Fig. 5. *Dissocians* populations in relation to parental morphometrics and the limits for *solitaria* and *gregaria*.
AP = Archico (14) parents
AF_1 = Archico (14) progeny

dimension towards the phase *solitaria* relative to the position of the discriminant of the reference 'cool' gregarious population (Fig. 6; Table 8). This shift was not as great as that for Archico (9) (Fig. 2, Fig. 6) which developed crowded in unshaded 'hot' conditions, but the Ailet (10) position in the 'phase' dimension closely corresponded to that for the seventh generation of laboratory adults bred

Table 8. *'D' values for populations Ahad (12), Adarit (6), Archico (14), Ailet (10) and Archico (13)*

Ahad (12)	'D' values	d.f.	Variance ratios	Probability
'Cool' *gregaria* male-Ahad Tug P female	6·849	3; 45	161·31	P<0·001
'Cool' *gregaria* female-Ahad Tug P male	3·732	3; 43	37·382	P<0·001
'Cool' *solitaria* male-Ahad Tug P female	7·354	3; 55	202·84	P<0·001
'Cool' *solitaria* female-Ahad Tug P male	4·318	3; 45	50·767	P<0·001
'Cool' *solitaria* male-Ahad Tug F_1 female	7·697	3; 64	302·71	P<0·001
'Cool' *solitaria* female-Ahad Tug F_1 male	3·118	3; 72	59·914	P<0·001
Ahad Tug P male-Ahad Tug F_1 male	1·514	3; 45	6·2408	P<0·001
Ahad Tug P female-Ahad Tug F_1 female	0·751	3; 37	1·7390	P>0·1
Ahad Tug F_1 male-Ahad Tug F_1 female	4·366	3; 59	92·691	P<0·001
Ahad Tug P male-Ahad Tug P female	5·416	3; 23	58·644	P<0·001
Ahad Tug P male-Ahad Tug F_1 female	5·752	3; 32	79·278	P<0·001
Ahad Tug F_1 male-Ahad Tug P female	4·126	3; 50	61·443	P<0·001
Adarit (6)				
'Cool' *solitaria* male-Cool *solitaria* female	6·277	3; 77	258·264	P<0·001
'Cool' *solitaria* male-Adarit male	3·361	3;139	107·16	P<0·001
'Cool' *solitaria* female-Adarit male	4·891	3;144	222·12	P<0·001
'Cool' *solitaria* female-Adarit female	2·798	3;146	73·031	P<0·001
Adarit male-Adarit female	3·550	3;218	231·04	P<0·001
'Cool' *solitaria* male-Adarit female	6·185	3;151	390·99	P<0·001
Archico (14)				
'Cool' *gregaria* male-Archico F_1 female	5·018	3; 56	120·35	P<0·001
'Cool' *gregaria* female-Archico F_1 male	4·661	3; 69	128·42	P<0·001
'Cool' *solitaria* male-Archico F_1 female	5·692	3; 66	173·85	P<0·001
'Cool' *solitaria* female-Archico F_1 male	5·966	3; 71	216·31	P<0·001
'Cool' *solitaria* male-Archico P female	5·951	3;165	373·94	P<0·001
'Cool' *solitaria* female-Archico P male	5·609	3;229	330·67	P<0·001
Archico F_1 male-Archico P male	3·154	3;228	102·19	P<0·001
Archico F_1 female-Archico P female	3·094	3;149	70·015	P<0·001
Archico P male-Archico P female	3·149	3;317	251·40	P<0·001
Archico F_1 male-Archico F_1 female	5·350	3; 60	144·10	P<0·001
Archico F_1 male-Archico P female	5·403	3;159	274·8	P<0·001
Archico P male-Archico F_1 female	4·846	3;218	183·99	P<0·001
Ailet (10)				
'Cool' *solitaria* male-Cool *solitaria* female	6·277	3; 77	258·264	P<0·001
'Cool' *gregaria* female-Ailet II male	4·799	3;131	199·60	P<0·001
'Cool' *solitaria* female-Ailet II male	6·814	3;133	418·68	P<0·001
Cool' *gregaria* male-Ailet II female	2·766	3; 91	53·762	P<0·001
Ailet II male-Ailet II female	3·728	3;157	174·39	P<0·001
'Cool' *solitaria* male-Ailet II female	3·572	3;101	105·90	P<0·001
Archico (13)				
'Cool' *solitaria* male-Cool *solitaria* female	6·277	3; 77	258·264	P<0·001
'Cool' *solitaria* male-Archico D_2 female	2·856	3; 58	34·642	P<0·001
'Cool' *solitaria* female-Archico D_2 male	7·259	3; 68	306·22	P<0·001
'Cool' *gregaria* male-Archico D_2 female	1·922	3; 48	14·252	P<0·001
'Cool' *gregaria* female-Archico D_2 male	5·370	3; 66	163·13	P<0·001
Archico D_2 male-Archico D_2 female	3·272	3; 49	41·804	P<0·001
'Cool' *solitaria* male-Archico D_3 female	1·840	3; 55	12·704	P<0·001
'Cool' *solitaria* female-Archico D_3 male	8·144	3; 68	385·46	P<0·001
'Cool' *gregaria* male-Archico D_3 female	1·860	3; 45	11·904	P<0·001
'Cool' *gregaria* female-Archico D_3 male	6·225	3; 66	219·24	P<0·001
Archico D_3 male-Archico D_3 female	3·013	3; 46	31·543	P<0·001

crowded by Hunter-Jones at a minimum night temperature of 28° C and a maximum day temperature of 34° C (Fig. 6). The parents of Ailet (10) and Archico (9), were in swarms and very probably had morphometrics closely similar to those for 'cool' phase *gregaria* locusts.

The population Archico (13), of highly heterogeneous history but ultimately of

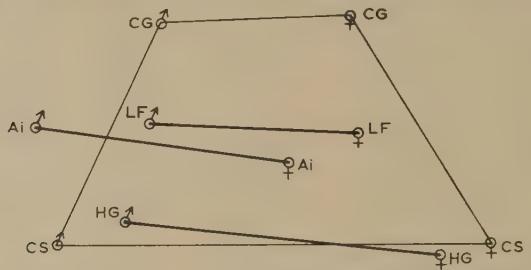

Fig. 6. *Gregaria* populations from hot conditions in the field and laboratory in relation to the limits for *solitaria* and *gregaria*.
Ai = Ailet (10); hot conditions but abundant shade.
LF = Laboratory data.

phase *dissocians* (p. 315), has been considered within the generalized distance diagram in relation to the relative position of the population with respect to the limits of phases *solitaria* and *gregaria* (Fig. 7; Table 8), and not to the parental morphometrics which were of two types. Morphometrically the two fledgling

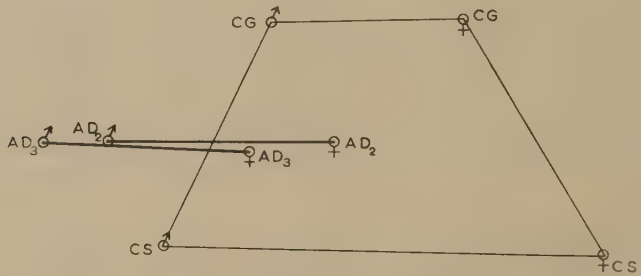

Fig. 7. *Dissocians* populations in relation to the limits for *solitaria* and *gregaria*.
AD_2 = Archico (13), sample D_2
AD_3 = Archico (13), sample D_3

samples obtained are of interest in that the positions of the lines representing the populations are displaced to the left, indicating the small sizes of the locusts (p.326).

(*e*) *Eye-stripe number*

Studies on the numbers of vertical stripes on the compound eyes were made only in a limited number of cases, but these indicate the possible value of this character in giving information additional to that given by the morphological characters *E*, *F* and *C* on the histories of populations. In the Akbanazuf (1) sample, five of the males (12%) and seventeen of the females (45%) had seven

eye stripes, the remainder having six. The corresponding percentages of males and females with seven eye stripes in the Halibai (11) parent and progeny samples were eighteen and thirty-three, and twenty-five and forty. In contrast, no males and 4% of females in the Archico (9) fledgling sample had seven eye stripes. The latter population was 'hot' *gregaria* and the others were 'cool' *solitaria* or *congregans*. Consequently, it does appear that this character can be of use in differentiating 'hot' *gregaria* populations from those of other histories when, on linear measurements the differentiation between such populations may not be great. On the data available it would seem that in 'cool' *solitaria* and *congregans* fledgling populations 33% or more of the females have seven eye-stripes whereas in 'hot' *gregaria* less than 5% may be of this type.

DISCUSSION

There is strong evidence that the morphometric characters of adults of the desert locust vary in relation to density and environmental factors associated with temperature, in ways which, upon the characters *E*, *F* and *C* only, are apparently opposite in effect, *i.e.* increased density during development moves the morphometric characters towards the 'cool' gregariform type, whilst increased temperature moves the characters towards the 'cool' solitariform type. As a consequence, morphometrics may be used for the measurement of phase and phase change, only if the environmental conditions under which particular populations developed are also taken into account. Such a procedure has not been adopted previously in morphometric studies on phase in locusts, and it has apparently been generally assumed that morphometrics are purely density-dependent. Some workers (p. 317), however, have already recognized the possibility of the influence of density-independent factors on morphometrics. Of the two methods of morphometric analysis, that of the ratios $E : F$ and $F : C$ and that of the generalized-distance addition of *E*, *F* and *C*, only the latter method can discriminate the different effects of density, temperature and other environmental factors upon the characters. Comparison of the two methods also shows that the multivariant analysis does not introduce the ambiguities presented in the 'phase' scale by the comparative use of the ratios $E : F$, $F : C$.

In the discriminant function diagram, though the density and temperature effects upon morphometrics were found to lie in a single plane, resulting in apparent confusion in 'phase' position, comparison of the sexual dimorphism represented by the length of the 'hot' *gregaria* and 'cool' *solitaria* discriminants largely resolved this ambiguity. The confounding along the phase dimension of the two factors is due to the high correlation of their effects on the morphometrics of the characters used. The use of canonical variates to separate the morphometric effects of temperature and density into two dimensions was considered. This method provides extra information on dimensions by the appropriate addition of multiples of both the 'group' and 'error' matrices. Only two of the three derived dimensions were significant and the 'biological' axes corresponding to temperature-density and sex-size difference were neither parallel to them nor at right-angles to

each other. The compressed elongated figure obtained by plotting sub-sample means was more difficult to interpret than the corresponding generalized distance diagram. Consequently, in morphometric studies on the desert locust it may be necessary either to substitute three other characters in which the above effects are less closely correlated, or to employ in addition to the three measurements used in the present studies at least one other such as *P* (length of pronotum at keel) which was shown by Misra, Nair & Roonwal (1952) to be a very good phase discriminant in *Schistocerca gregaria*. The number of eye stripes could also be used, as might other characters to which numerical values other than linear measurements can be given.

Within the limits of the data available, some associations emerge between the apparent morphometric differences and the different histories of the populations analysed. Comparison of the various diagrams shows that there is variation in the positions of the discriminant lines representing the different populations from left to right. This variation in position is due to the size differences of the populations. The relationship of the positions of the different sexes along the horizontal dimension represents sex-size differences, and these change according to the position of the sex discriminant in the diagram. The size of the characters may be related to the amount of available food but other conditions may also be involved. Figs. 3 and 4 illustrate the discriminant lines of populations adjudged on independent criteria to be of phase *congregans*, whilst Figs. 5 and 7 relate to populations in which dissociation is known to have occurred. By comparison, it is readily seen that in the former there is a displacement of the lines to the right, indicating the larger size of the adults, whilst the displacement to the left in the latter diagram correspondingly indicates the smaller size of the *dissocians* types. The fledgling population from Ailet (10) (Fig. 6), which was of phase *gregaria* but exposed to 'hot' though shaded environmental conditions, was reasonably similar to the phase *dissocians* populations in that the individuals were relatively small. The fledglings of phase *gregaria* from a 'hot' developmental environment with little shade, Archico (9) (Fig. 6) were similar to those of 'cool' developmental phase *solitaria* in respect of size but the sexual dimorphism appeared to be less.

The number of populations studied is too small to cover the intermediate stages in the morphometrical expressions of the effects of congregation, dissociation and 'temperature'. The examples studied, however, are suggestive of certain trends in the diagrams which appear to correspond to the different population histories. If the mid-point of each 'horizontal' line representing the different populations, which can be assumed to indicate size independently of sex differences, is plotted as in Fig. 8, the morphometric trends become apparent and suggest that these three dynamic categories of populations may be differentiated on the basis of the position of the relevant discriminant line along the horizontal size dimension. The relatively small size of some locusts may be due to the quality and quantity of food available, and the small size of phase *dissocians* samples, under certain circumstances, may be related to similar conditions that are not optimum for maximum growth and development. Conversely, congregation might occur

under reverse food conditions, so that there could be a correlation between the state of the habitat and phase change. From the field data, it would seem that relatively 'hot' environmental conditions affect morphometrics in a manner similar to that of dissociation. The small morphometrics of the crowded locusts at Ailet (10) may be due directly to a low-value food factor, which in itself was controlled by the 'hot' conditions. Hunter-Jones's laboratory data on adults bred crowded in a similar temperature range to that of Ailet (10), but given a good supply of food, were much larger, as can be seen by the position of the discriminant along the horizontal dimension (Fig. 6). Discrimination of 'hot' crowded locusts from 'cool' dissociating locusts might be achieved by comparison of their respective sexual dimorphism. However, the number of eye stripes appears, on the evidence available, to give a better means of discriminating 'hot' phase *gregaria* from 'cool' phase *dissocians*, where these types are otherwise morphometrically similar. *Schistocerca* adults with seven eye stripes originate from hopper popula-

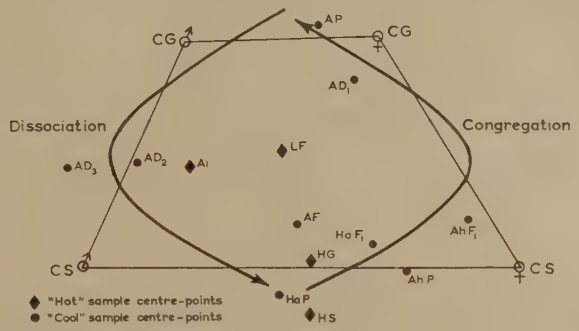

Fig. 8. Possible congregation, dissociation and 'temperature' effects in relation to the limits for *solitaria* and *gregaria*.

tions of low density, whereas forms with six eye stripes are present almost to the exclusion of the seven-eye-stripe form when the hoppers have been in bands throughout development. Thus, morphometrically solitariform adults which have six eye stripes have probably developed from gregarious hoppers under 'hot' environmental conditions.

Comparison of the positions of the various discriminants in the vertical 'phase-temperature' dimension in the different diagrams provides further information on the population histories. The discriminants of the Halibai (11) and Ahad (12) fledglings show only slight shift, along the vertical dimension towards phase *gregaria*. Congregation had occurred in these populations, respectively, in the hopper stage only and in the hopper and adult stages. The Adarit (6) fledglings' discriminant, on the other hand, moved much further up the 'phase' dimension, though still not giving full expression to extreme gregariform morphometrics. Its population history was similar to that of Ahad (12) in that its parents were in loose swarms and had hopper characters of a similar type, though its adult morphometrics were not available. However, unlike Ahad (12), the fledglings arose

from hoppers which had been in bands since the time of hatching. The population in which dissociation occurred at the time of hatching, amongst hoppers that were the progeny of swarms of morphometrically *gregaria* adults, showed a very large shift down the vertical dimension towards the morphometric characters of phase *solitaria* (Figs. 5, 8). Thus, the morphometric changes during dissociation, cover a large part of the known range after complete dispersal during the hopper history only. In the process of congregation and gregarization, on the other hand, the full morphometric expression of phase change appears to require much longer than one complete generation in highly crowded conditions as adults and hoppers. This cumulative effect of density has been demonstrated in the laboratory by Hunter-Jones (1958). Further, this suggestion has a parallel in the statement of Albrecht & Blackith (1957) that *Nomadacris septemfasciata* requires two complete generations of crowded conditions to attain the full morphological expression of *gregaria*.

The effect of 'hot' conditions on the rate of shift down the vertical dimension towards solitariform morphometrics can be inferred to be similar to that of dissociation by comparison of the positions of the discriminants of the shaded 'hot' crowded and unshaded 'hot' crowded samples. This effect may be largely that of temperature. However, the rate of shift in the reverse direction is not known since a population with a history of parents in 'hot' crowded conditions with progeny in 'cool' crowded conditions was not available. Hence a parallel cannot be drawn between the corresponding effects on rates of morphometric shift of increasing density and decreasing temperature and conversely of decreasing density and increasing temperature.

The method of multivariant discriminant analysis adopted in this paper has been shown to be superior to previous analytical techniques using single characters and ratios of pairs of characters, because it has involved the identification of the correlated morphometric effects of the various factors and their simultaneous presentation for interpretation in geometric form. The removal of the identified morphometric effects of factors other than density from the error matrix or unit of measurement reduces its size in comparison with that provided by analysis of the phase contributions of character ratios. This reduction in the unit of measurement increases the sensitivity of 'phase' discrimination and resolves the ambiguities in the 'phase' scale presented by the analysis of variance of the ratios $E : F$ and $F : C$. Thus, taking the $E : F$ and $F : C$ ratios shown in Table 2, the 'hot' *gregaria* population Archico (9) may be regarded as being of equivalent phase status with the Akbanazuf (1) 'cool' *solitaria* sample on the basis of male $E : F$ but slightly more gregarious than the latter because of its higher female $E : F$ and low $F : C$ ratios in both sexes. Hence different conclusions may be drawn according to the pairs of characters chosen. Extending the comparisons to E, F and C of each sex considered separately, the drawing of conclusions becomes more complex because the relative values of the characters are reversed in the sexes. If only one pair of these characters, *e.g.* male $E : F$ ratio, is selected and is used in conjunction with eye-stripe data, it may be concluded that although the Archico

(9) sample is *solitariform* in $E : F$ it is in fact 'hot' *gregaria* because of the small proportion of individuals with seven eye stripes. A different confusion occurs in the case of the parent adults of Ahad (12) and the fledglings at Archico (14) which had male $E : F$ ratios of 2·02-2·04, yet their histories were probably different in that one was possibly *solitaria* or early *congregans* whilst the other was *dissocians*. Similarly the $E : F$ ratios of the Ahad (12) and the Archico (13) fledglings were 2·11 and 2·10, but they were known on separate evidence to be of *congregans* and *dissocians* phase respectively. Eye-stripe data were not obtained for these populations but it is evident that, in terms of male $E : F$ ratios alone, different histories cannot be distinguished and that by using many characters separately the conclusions differ. The complete failure of ratio analysis to discriminate between the various morphometric effects of congregation, dissociation and temperature is due to the elimination of the sex-size dimension, resulting in the confounding of these various morphometric effects along a single dimension, the so-called 'phase-scale'. Multivariant analysis, on the other hand, maintains the dimension which is concerned mainly with sex-size differences and it appears that both the discriminant measure of sexual dimorphism and the position of the central point of the sex-size discriminant may reveal differences in the morphometric effects of congregation, dissociation and temperature. The initial labour of calculation of multivariant analysis is heavier than for the other technique, but the introduction of other samples for further reference points or for comparison involves far less calculation. The method of analysis used in this paper also allows the consideration of any number of characters for each sex simultaneously and the expression of relative differences between samples graphically in a way that holds some promise of differentiating between population histories even where there may be superficial morphometric resemblances. Multivariant analysis has identified and made the maximum possible use of the morphological expressions of the various environmental effects on the populations described. Still better information could be obtained by the use of characters common to both hopper and adult stages as well as additional characters in which the effects of the various factors were less well correlated.

It can be seen that in locust studies it is of considerable practical value to be able to distinguish not only the extreme phases *solitaria* and *gregaria*, but also the direction of phase change or differences between phases *congregans* and *dissocians*. Such knowledge is important in studies on the ways in which swarms may form or break down and in which outbreaks may commence or cease. From evidence produced in this paper it is clearly necessary, at least in the case of the desert locust, to be able to detect also the effects of the environment upon morphometric phase characters, particularly where these may mask the morphological expressions of purely density-dependent conditions. Hopper morphology in *Nomadacris septemfasciata* (Albrecht & Blackith 1957) and hopper coloration in the desert locust (Stower 1959) provide useful indications, but on the frequent occasions when adults only are observed, the measurable characters are the end-products of various environmental factors operating during the previous history

of the insects. This paper has shown that considerable information on the previous history of a locust sample can be obtained by the application of a suitable method of analysis to appropriate adult characters and their comparison with the morphometric reference points of samples of known history.

SUMMARY

1. The histories of fourteen populations of the desert locust are briefly described. The populations are classified, according to their histories, as being of phases *solitaria*, *gregaria*, *congregans* or *dissocians*. The temperature conditions during development are also taken into account.

2. Three linear measurements of body parts of both sexes in samples of adults from the populations studied are used for multivariant analysis. The advantages of this method of morphometric analysis over the methods previously adopted in locust studies are discussed.

3. The results of the analysis are expressed geometrically, and the morphometric discrimination between *solitaria* and *gregaria* populations is shown under different conditions of temperature. The morphometric relationships of *congregans* and *dissocians* populations to these limits are described and discussed. It is tentatively concluded that the method of analysis and its geometrical expression provide a means of using morphometrics to differentiate between populations of the desert locust of different histories.

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THE FOOD OF *RATTUS NORVEGICUS* BERK. IN AN AREA OF SEA WALL, SALTMARSH AND MUDFLAT

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(With 1 Figure in the Text)

It has long been known that rats, living independently of man, occur along the coast of Britain, but relatively little information is available about their food. Most of the records can be summed up in the words of Barrett-Hamilton & Hinton (1910-21, p. 622); 'on the seashore the food is what is cast up by the sea, together with prawns, shrimps, shellfish, eggs and young of sea birds, and vegetable matter'. Further observations are, however, available from the Islands of Norderoog (Steiniger 1948) and Scharhoern (Habs & Heinz 1951), off the west coast of Germany. On both islands, not only did the rats eat the eggs of many birds, but they also (particularly on Norderoog) caught and ate live adult birds. The seeds of *Elymus arenarius* L. (Norderoog and Scharhoern) and *Chenopodium* spp. (Norderoog) were eaten during the late summer and autumn. Steiniger also mentions that in late December apparently almost all the plants on Norderoog were being eaten, but particularly striking were traces of gnawing at the rhizomes of *Triglochin maritima* L.

On these German islands, both of which are bird sanctuaries, observations on the rats were incidental to rat control to protect the birds. In the present study it was possible to make records of food for a whole year in a rather different type of coastal habitat on Bridgemarsh Island in Essex, where breeding birds were few and where occurred only three of the twenty-nine angiosperms noted from Scharhoern.

DESCRIPTION OF BRIDGEMARSH ISLAND

About 10 miles from its mouth, the River Crouch, here $\frac{1}{4}$ mile wide, flows along the southern edge of Bridgemarsh Island. To the north the island is cut off from the mainland by a winding creek 400 to 500 ft across. Once good farmland, Bridgemarsh today is a *Spartina*-covered mud flat of some 250 acres, dissected by numerous drainage channels and surrounded by 5 miles of sea wall. Outside the wall, which at the most is 4 ft high and in many places is washed away, lie stretches of saltmarsh, 80 acres in all. Just within the sea wall and along its whole length is a strip of less mature saltmarsh only a few feet wide. At normal high tides the whole of the interior of the island is flooded leaving only the sea wall and surrounding saltmarsh uncovered.

Detailed investigations were confined to $1\frac{1}{2}$ miles of sea wall and adjacent land at the east end of the island. The plants of this area are listed in Table 1.

No attempt was made to enumerate all the animal species but some are mentioned later.

OBSERVATIONS ON THE RATS

The brown rat (*Rattus norvegicus* Berk.) was present along the entire northern and part of the southern side of the island. The rest was not searched, but almost certainly harboured rats since its composition was similar. Rats were, however, absent from the salt marsh and seawall of the mainland to the north of the

Table 1. *The plants of the east end of Bridgemarsh Island*

	Abundant or common	Occasional or rare
Mud flats	*Aster tripolium* L.	
	Enteromorpha	
	Salicornia	
	Spartina townsendii H. & J. Groves	
Sea wall	*Agropyron pungens* (Pers.)	*Allium vineale* L.
	Atriplex hastata L.	*Anthriscus neglecta* Boiss. & Reut.
	A. littoralis L.	*Atriplex patula* L.
	Beta vulgaris L.	*Cirsium vulgare* (Savi)
	Bromus mollis L.	*Dactylis glomerata* L.
	Cardaria draba (L.)	*Galium aparine* L.
	Ceratodon purpureus (Hedw.)	*Geranium dissectum* L.
	Cladonia	*Lactuca serriola* L.
	Festuca rubra L.	*Rumex crispus* L.
	Halimione portulacoides (L.)	*Senecio erucifolius* L.
	Poa angustifolia L.	*S. vulgaris* L.
	Poa trivialis L.	*Vicia sativa* L.
		V. tetrasperma (L.)
Saltmarsh	*Armeria maritima* (Mill.)	
	Aster tripolium L.	*Cochlearia anglica* L.
	Festuca rubra L.	*Parapholis incurva* (L.)
	Halimione portulacoides (L.)	*Spartina townsendii* H. & J. Groves
	Limonium vulgare Mill.	*Spergularia salina* J. & C. Presl.
	Plantago maritima L.	*Suaeda fruticosa* Forsk.
	Puccinellia maritima (Huds.)	
	Salicornia	
	Spartina maritima (Curt.)	
	Suaeda maritima (L.)	
	Triglochin maritima L.	
River	*Ascophyllum nodosum* Le Jol.	
	Fucus vesiculosus L.	

island. That to the south was not visited. The rats made their burrows in the clay soil of the wall. Excavation of four of these showed that they varied from a single tunnel about 6 in. long ending in a grass-lined cavity 8 in. in diameter, to quite a complex system of tunnels with several entrances and nest chambers. The entrance holes were joined on the surface by runs along the sides and top of the wall. The runs on the top were tunnelled through sea couch grass (*Agropyron pungens*) and had frequent small 'lay-bys'. These, judging by the food remnants, were used particularly as feeding places as also were many cavities in the sides of the sea wall. Away from the wall some runs meandered for quite long distances

through the *Spartina*, finally petering out. Those across the saltmarsh usually led directly to the nearest small drainage channel, but rat footprints were often numerous on the mud just at the outer edge of the island.

Four to 8 hours were spent on the island roughly once every month from May 1956 to May 1957. Observations were made on food remnants on rat runs and damage to growing plants, but emphasis was placed on collecting fresh droppings for later examination. Droppings were mainly found in small groups on the rat runs. Each group, presumed to have been made by one rat, was placed in a

Table 2. *Results of the analysis of rat droppings*

	24 May	22 June	8 Aug.	4 Sept.	26 Sept.	29 Oct.	28 Nov.	31 Dec.	30 Jan.	27 Feb.	26 Mar.	25 April	21 May
Number of samples	13	23	5	31	44	44	45	50	44	34	16	12	11
MONOCOTYLEDONS													
Entirely	0	4	1	13	7	9	3	3	8	12	6	1	3
Mainly	5	11	3	7	12	23	20	13	27	20	8	9	4
Moderate	7	4	0	9	19	11	18	24	9	2	1	2	2
Little	1	4	0	2	6	1	2	5	0	0	0	0	1
DICOTYLEDONS													
Entirely	0	0	0	0	0	0	1	3	0	0	0	0	0
Mainly	0	0	0	0	0	1	12	12	0	0	0	0	0
Moderate	0	0	0	3	12	27	17	20	4	2	1	0	0
Little	0	0	0	4	11	5	11	6	7	9	1	1	0
VERTEBRATES													
Entirely	0	0	0	0	0	0	0	0	0	0	0	0	0
Mainly	0	0	0	0	0	0	0	0	1	0	0	0	0
Moderate	0	0	0	0	0	1	0	1	1	1	0	1	0
Little	0	0	0	2	1	1	0	0	2	3	0	1	0
CRUSTACEA													
Entirely	0	0	1	0	0	0	0	0	0	0	0	0	0
Mainly	3	4	0	3	18	3	0	2	5	1	1	0	2
Moderate	4	6	1	7	11	12	3	11	14	5	1	1	4
Little	5	8	1	4	4	7	7	4	16	9	6	9	1
INSECTS													
Entirely	0	0	0	0	0	0	0	0	0	0	0	0	0
Mainly	0	0	0	0	0	0	0	0	0	0	0	0	0
Moderate	4	7	0	5	1	0	0	1	0	0	0	0	2
Little	4	5	2	7	13	0	5	1	0	1	2	5	2

separate glass tube and preserved in 70% methylated spirits. Subsequently only one dropping from each tube was examined. This was done to ensure that the analysis would reflect as near as possible the feeding habits of the whole population, rather than a few individuals. The droppings examined were teased out under methylated spirits in a petri dish and viewed through a binocular microscope. Notes were made on their contents, including a rough visual estimate of the quantity of each component; little (1-5%), moderate (6-50%), mainly (51-99%) and entirely (100%). The results of this analysis are summarized in Table 2. From the data have been calculated monthly frequency and quantity indices for each

food category and these are plotted in Fig. 1. The frequency index is the number of droppings containing a particular food divided by the number of droppings examined. The quantity index is the quantity of a particular food divided by the quantity of all foods. For this calculation the quantity of a food in a dropping is taken as being the central point of the quantity group in which the food was put. Thus a food marked as little (1-5%) is regarded as having a quantity of 2·5.

The categories into which the foods have been grouped were largely determined by the ease with which the normally very small fragments of material could be identified. In many cases, however, greater precision was possible and these are mentioned below.

(*a*) *Monocotyledons*

Apart from seeds of sea couch grass which occurred to a small extent during the autumn, all the easily identifiable grass remains (ligules, flowers and seeds) in the droppings belonged to *Spartina*. Since no damage to *S. maritima* was found there

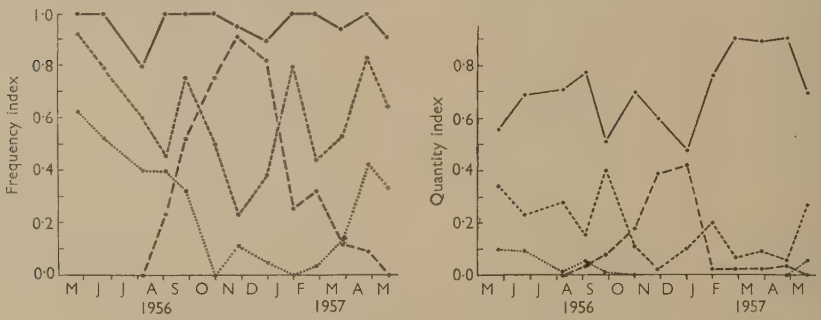

Fig. 1. Seasonal changes of food remnants in droppings: ●———●, monocotyledons; ●— —●, dicotyledons; ●- - -●, Crustacea; ●.....●, insects.

is little doubt that they came from *S. townsendii*. Chewed fragments of this plant were found throughout the year along the runs in the interior of the island. The stems were bitten through generally 2 or 3 in. above the ground and apparently (except for flowers and seeds during the summer and autumn) only the lower parts of the stems were eaten. The rest of the shoots were washed away and formed a large portion of the debris along the tideline within the sea wall.

(*b*) *Dicotyledons*

Seeds were present in the droppings from September to January and all were identified at least to genera: *Suaeda maritima* (September-November), *Atriplex* (October), *Halimione* (December), and *Salicornia* (November-January). Very few fragments of leaves were found and no attempt was made to identify them. The only dicotyledon that showed signs of damage by rats was *Aster tripolium*. Feeding on this plant lasted from October to February, by which time nearly all the plants on the edge of the mudflat close to the sea wall had been attacked. Only the parts

of the rhizomes projecting above the mud were eaten, and the leaves were left lying close by. The plants, however, quickly recovered during the spring and suffered no further damage.

(*c*) *Algae and Bryophytes*

There was no evidence of any feeding on seaweeds, lichens or moss.

(*d*) *Vertebrates*

Vertebrate tissue in droppings was infrequent and nearly always associated with feathers, which no doubt were the result of rats feeding on the occasional dead bird washed up by the tide. The only nesting birds were mallards (*Anas platyrhyncha* L.). In May 1956 two nests were found at the edge of a rat run that did not seem to be very much used. One had fragments of shell in it and the other had eggs just hatching. In April 1957 three nests were noted. All were in thick grass on the top of the sea wall within 1 or 2 ft of well used runs, but shielded from them by grass. One contained thirteen nestlings and the others eleven and nine undamaged eggs. Rats did not appear to have disturbed these nests but it is possible that they did not detect them.

Voles and shrews were present on the island, but the only evidence that either of these were eaten was the remains of two freshly eaten shrews on a rat run in May 1957.

(*e*) *Crustacea*

The most obvious food remnants on the runs were broken shells of the shore crab, *Carcinus maenas* (Pennant), which gave the impression that rats ate them in large numbers. However, only few freshly eaten crabs were found on any one visit and very few pieces (mainly gills) were recovered from droppings. The crustacean most eaten was the sandhopper, *Orchestia gammarella* (Pallas). Some droppings composed almost entirely of fragments of this species were pink in colour. Woodlice were fairly common on the sea wall, particularly *Armadillidium vulgare* (Latreille) on the rat runs, in many cases apparently feeding on rat droppings. Since, however, no trace of woodlice was found in droppings it seems that rats do not eat them.

(*f*) *Insects*

During the spring and summer, the insects most frequently eaten were ground beetles (Carabidae). Very few insects were taken during the winter and these were mainly fly larvae, probably from the rats' own nests and burrows.

(*g*) *Others*

Other invertebrates eaten included four minute whole snails, one leg of a harvestman and one minute spider and one centipede. Also, in January 1957, a cluster of whelks' eggs apparently chewed by rats was found on a run. A relatively

small number of fragments were not identified and not obviously placeable in any of the groups above. As they would not affect the general picture these have been ignored.

DISCUSSION

Before discussing the foods that were eaten it is worth noting that seventeen of the twenty-five abundant or common plants and all seventeen of the occasional or rare plants (except perhaps *Atriplex patula*) were apparently not eaten by rats. Although Steiniger does not list the plants of Norderoog, his finding that the rats were, in late December, apparently feeding on almost all the available plants is probably in direct contrast to the situation on Bridgemarsh. It is likely that this indiscriminate feeding was due to food shortage, since in July there were calculated to be at least 5000 rats on Norderoog in an area of less than 35 acres, and only 2000 to 3000 had been killed before December.

The results of the dropping analyses are given in the form of both frequency and quantity indices as these are to a certain extent complementary to one another. The quantity index shows the relative amounts of different foods in the droppings and the frequency index shows whether a particular quantity is made up by occasional or more frequent feeding. Both indices, as might be expected, indicate similar seasonal changes in food, and in general appear to follow changes in abundance of the types of food involved. Thus *Spartina* was eaten throughout the year, seeds of dicotyledons mainly in the autumn, and insects and crustacea were least eaten during the winter. On the other hand the rhizomes of *Aster tripolium*, perhaps because of their role as food storage organs, were apparently only attractive to rats during the autumn and winter.

The nature of droppings, the few samples in some months and the rather rough estimates of quantity make it difficult to be sure how accurately the quantity indices reflect the relative quantities of the different foods eaten. Despite this, however, there can be little doubt that *Spartina townsendii* served as a main food source throughout the year. More recent observations have shown that feeding on *S. townsendii* is not a local habit confined to Bridgemarsh Island. It occurs, though to a lesser extent, at Steart Island in Bridgwater Bay (Drummond, Prestt & Redfern, unpublished) and surveys of short stretches of the northern shores of the estuaries of the rivers Blackwater, Deben and Stour indicate that it is probably prevalent in East Anglia. In fact, in the latter areas, although some traces of rats were found where *S. townsendii* was absent, they were more common in areas where *Spartina*-covered mud flats came right up to the sea wall. This suggests that *S. townsendii* may affect the distribution of rats in some coastal areas in much the same way as cereals do on agricultural land.

ACKNOWLEDGMENTS

It is a pleasure to record my thanks to many of my colleagues for their help, especially Mrs M. Rowe and Mr R. Redfern.

SUMMARY

1. A one year study of the food of *Rattus norvegicus* in an area of sea wall, saltmarsh and mud flat is described.

2. Information about the food was obtained from traces of feeding and the analysis of droppings.

3. The principal food throughout the year was *Spartina townsendii* supplemented mainly by varying amounts of dicotyledonous plants, crustacea and insects.

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OBSERVATIONS ON THE RESPONSE OF SOME BENTHONIC ORGANISMS TO POWER STATION COOLING WATER

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(With 2 Figures in the Text)

Very little is known about the response of benthonic and settling organisms to the activities of power stations. A few sporadic observations on this subject were given in the previous paper (Markowski 1959) although the main subject there was the response of zooplankton to raised temperature, and chlorination applied by the power stations. The intention of this paper is to give more information regarding the behaviour and response of benthonic and settling organisms in the intake and the outfall area of a power station. The investigation was started in October 1957, and terminated in October 1958 in Cavendish Dock at Roosecote Generating Station, Barrow-in-Furness, Lancashire, giving an annual cycle of the occurrence of particular species.

MATERIAL AND METHODS

Twelve concrete slabs $12 \times 12 \times$ about 1 in. thick were placed, six in the intake, and six in the outfall water at a depth of about 4 ft (122 cm). They were facing west, so that the light regime was the same in both places. Each slab was provided with an iron ring and a rope, which allowed it to be lifted gently for examination. The top surface of the slabs was fairly smooth, but the bottom surface was more uneven. The unevenness of the bottom surface, and of the substratum formed excellent shelter for organisms with a predilection for this kind of environment.

The slabs were lifted and examined every month. The results of these examinations and the respective dates are shown in Tables 1 and 2. The attached organisms were partially removed from the slabs, leaving the rest undisturbed, and the motile forms were washed out and collected. They were examined *in vivo*, then fixed and stored in 5% formaldehyde solution in the dock water for further examination. The whole collection of the organisms found on the slabs in the intake and the outfall areas, after being identified, was presented to the British Museum (Natural History).

THE ENVIRONMENT

(*a*) *The dock*

Cavendish Dock is an artificial water-reservoir, completed in 1878 (Barnes 1951). Its surface area is 144 acres (583 355 m^2); the minimum depth is 7 ft (213 cm) and the maximum 10 ft (305 cm). The volume of the dock water fluctuates between 270 million gallons (1227×10^6 l.) and 390 million gallons (1773×10^6 l.).

In September 1953 the Roosecote Generating Station started taking dock water

for cooling purposes at the rate of 1 400 000 gal/h ($6{\cdot}4 \times 10^6$ l. h) when using one pump only, or at the rate of 5 600 000 gal/h ($25{\cdot}4 \times 10^6$ l. h) when in full operation. Practically the whole volume of the dock water could be then circulated through the station in 48 h when the depth of the dock water is 7 ft or in 70 h at the highest water level of 10 ft.

In its southern part, Cavendish Dock is connected by a sluice with two gates

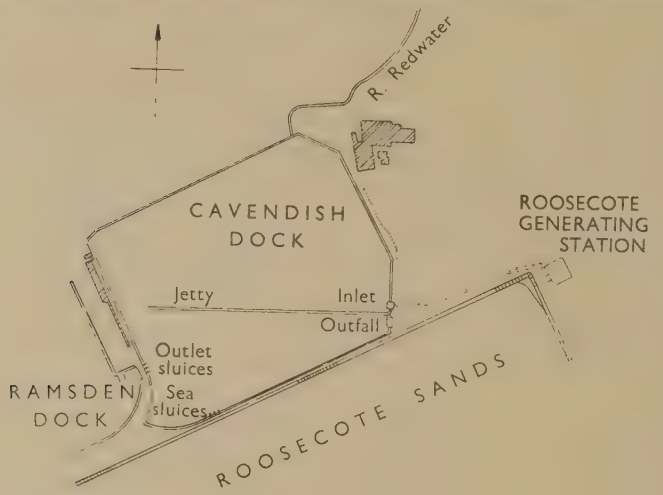

Fig. 1. Plan of Cavendish Dock.

each of about 2·9 ft² (82·5 cm²) with Roosecote Sands and Walney Channel, and through it with Morecambe Bay (Fig. 1). Another double sluice of $2{\cdot}9 \times 3{\cdot}6$ ft ($82{\cdot}5 \times 105$ cm) and $2{\cdot}9 \times 2{\cdot}3$ ft ($82{\cdot}5 \times 67{\cdot}5$ cm) in the western part of the dock drains the water into Ramsden Dock. The sea water, therefore, comes into the dock through the southern sluice and its surplus, if any, is drained by the western sluice back into the sea. The sluices are not opened at regular intervals.

Table 1. *Chemical analysis of R. Redwater (p.p.m.)*

pH	7·7	Nitrate as N	2·6
Alkalinity $CaCO_3$	189·0	Chloride as Cl	60·3
Calcium as Ca	87·7	Total iron as Fe	0·012
Magnesium as Mg	15·0	Silica as SiO_2	7·1
Zinc as Zn	0·012	Phenol as C_6H_5OH	0·14
Phosphate as PO_4	0·21		

Another water supply comes by the small river called Redwater, into the northern corner of the dock. This freshwater supply also varies with the season and the amount of rainfall. The flood water and some domestic wastes are also directed through that river into the dock, but this does not cause any pollution detrimental to the organisms of the dock. The analysis of the water from the river Redwater is given in Table 1.

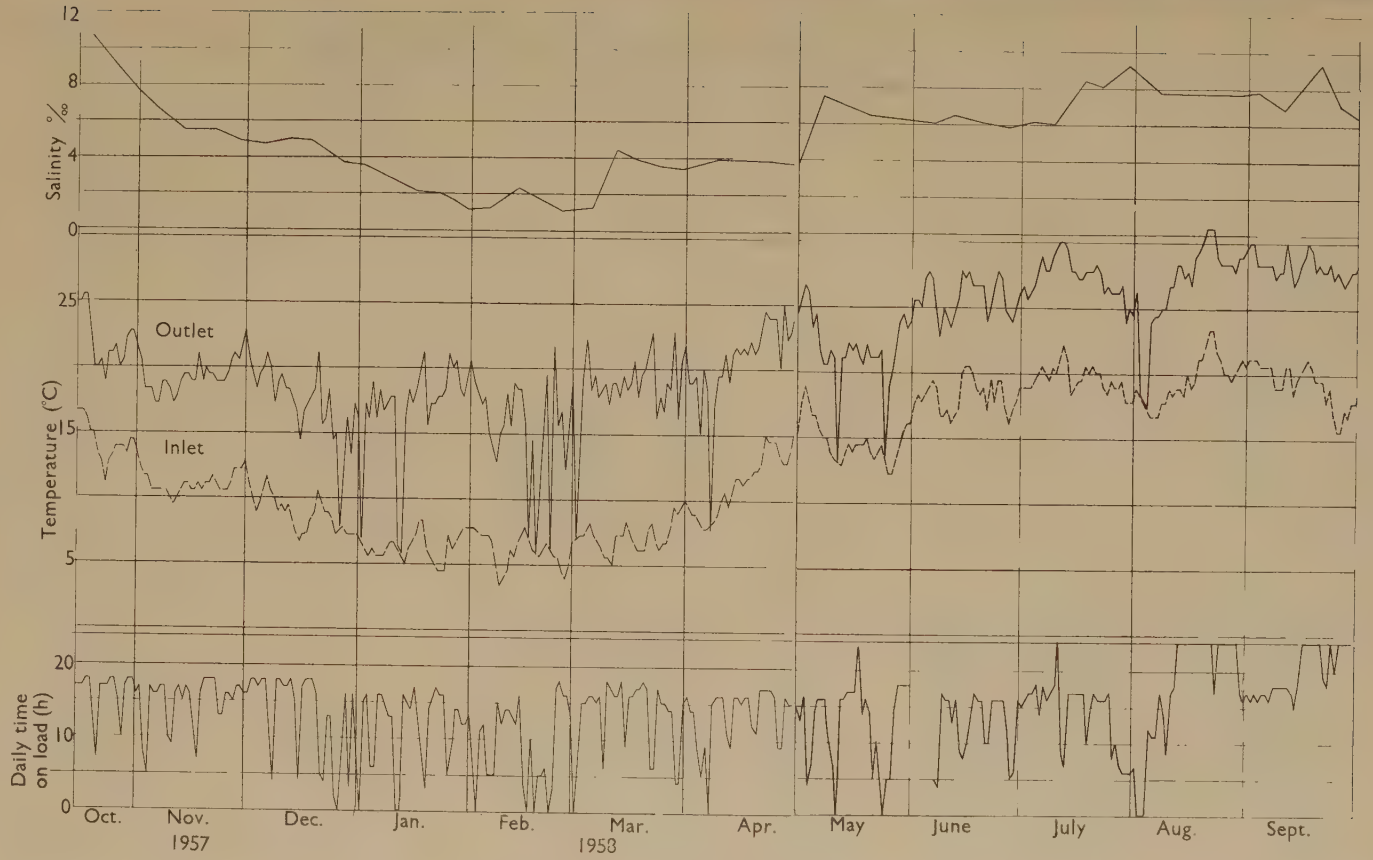

Fig. 2. The salinity and temperature in Cavendish Dock during the investigation, and the cycle of operation of the power station.

Because of the dock's almost closed character, and of its freshwater supply by the river Redwater and by rainfall, the salinity of the dock water varies considerably. The dock water has been analysed for salinity every week since the station has been in operation. According to the records, the lowest and the highest salinity per mille for each year were: 1954, 1·24 (Nov.); 1955, 15·0 (July) and 25·0 (Dec.); 1956, 8·6 (Feb.) and 25·4 (July); 1957, 4·12 (Feb.) and 22·0 (Aug.); 1958, 1·0 (Feb.) and 9·0 (Sept.). These figures show that the salinity is extremely variable since it depends on weather conditions. During the experiment (1957-8) the salinity dropped considerably lower than ever before (Fig. 2).

The extremes of temperature (° C) recorded at the power station over the same period were: 1954, 8·3 (Dec.); 1955, 6·1 (Feb.) and 25·5 (July); 1956, 7·2 (Feb.) and 25·1 (July); 1957, 6·1 (Dec.) and 16·7 (Oct.); 1958, 3·3 (Feb.) and 23·3 (Aug.).

The pH of the dock water was about 8·1. During this investigation the oxygen in the dock water was never less than 90% of the saturation value.

(*b*) *The environment around the slabs*

The intake and the outfall areas where the slabs were placed represent two different environments separated by a concrete jetty (Fig. 1). In the intake, the environment is identical with the rest of the dock in annual fluctuations. The only factor new to it is the velocity of the water when the station operates, when the water is pumped into the plant with a constant velocity of 1·1 ft sec (33·5 cm sec).

In the outfall the slabs are exposed to higher temperatures, variable velocity, turbulence, and chlorination. When the station operates, the temperature of the water in the outfall rises about 10° C above the seasonal temperature of the dock water, and returns to it when the station stops. There are, therefore, thermal pulses connected with the station's activities.

The velocity of the outfall water varies with the number of turbines in operation; if one is used the velocity is 1 ft/sec (30 cm sec), and when two turbines operate it rises to 2·7 ft/sec (83·3 cm/sec).

When the station works, the movements of the water in both areas can be compared to a fluvial environment. Using the classification of Tansley (1939) this fluvial habitat with the velocity of the water at 1·1 ft/sec (33·5 cm sec) corresponds with a river with a partly silted gravel bed; with the velocity of the water at 2·7 ft sec (82·3 cm sec) conditions approach those in a torrent with an unsilted bed of shingle. As the water discharged by the outfall culverts runs through a kind of channel the turbulence there is very powerful bringing undoubtedly more oxygen around the slabs in the outfall area than in the intake.

The duration of the operation of the station is shown in Fig. 2 in hours per day during this investigation, together with the rise of temperature it produced throughout the year.

Once a day, between 10·0 a.m. and noon, chlorine at a concentration between 1 and 2·5 p.p.m. is injected into the condensers. There are eight condensers to be treated for 7 min each at the rate of 500 lb (226·8 kg) of Cl_2 every 24 hours. The

chlorine content of the cooling water falls very rapidly, so that on rare occasions only does the outfall water contain 0·1 p.p.m. residual chlorine.

It should be emphasized that some of the organisms pumped into the station through the intake are exposed to raised temperature and chlorination before being discharged into the outfall, and therefore to the area of the slabs.

FAUNISTIC OBSERVATIONS

Little is known about the fauna of Cavendish Dock. Because of very peculiar environmental conditions the specific composition may vary, according to the fluctuations in salinity, and also the invasion of marine and freshwater forms into the dock. Though the investigations on the fauna of the dock were commenced only 3 years ago, and on a small scale, every year some unexpected species were collected. During the compilation of this paper *Mercierella enigmatica* was found on the slabs and in the tanks of the power station; also *Engraulis encrassicholus* of various sizes and its eggs were found in the dock, as was *Solea solea*, never previously recorded here.

The faunistic results obtained using the experimental slabs are shown in Table 2. Some twenty-six different forms were found, nineteen on the intake and twenty-six on the outfall slabs. There were two species of alga, and one species of fish; the rest were invertebrates. Out of the twenty-six forms, seven juvenile stages could not be specifically identified.

The first settled organisms were observed in the outfall slabs in November 1957 when numerous growths of young *Actinia* sp. appeared on the bottom surface of the slabs. They were about 5 mm in diameter and of a fleshy-red colour. They gradually decreased in number, turning to a chocolate-brown colour and perished in December. They were followed by *Cordylophora lacustris* in January 1958. In April an intense growth of algae, *Enteromorpha intestinalis* and *E. ahlneriana* developed, giving shelter to various species listed in Table 2. The filaments were about 20 in. (50·8 cm) long, and so thick that on three occasions three and five young eels about 7 cm long were lifted with the slabs. No growth of *Enteromorpha* was noticed on the intake slabs. The filaments of algae were covered with masses of colonial vorticellids. *Mytilus edulis*, absent in the intake, appeared in the outfall slabs in November 1957 and disappeared in May 1958; only ten specimens were found, about 2 cm in length. *Mytilus edulis* were very abundant in the dock in previous years, but have disappeared from the dock for some unknown reasons in the period of 1957-8. In 1956 75 tons of *Mytilus edulis* were removed from the culvert of the power station. According to some observations of Mr S. M. Musgrave, the station chemist, the mass occurrence of mussels in the dock is connected with salinity. They usually disappear when the salinity drops to a low level.

Polyzoa, mainly *Conopeum spiculatum*, appear in February. Because of the competition with the species of *Enteromorpha* the colonies are hampered in growth and disappear in July from the outfall. In the intake these Polyzoa show very intense growth and give shelter to various motile forms (Table 2). They compete with colonies of *Cordylophora lacustris*, which flourish in the intake feeding on

Table 2. *Organisms found on the slabs*

	Date of collection									
	1957		1958							
Intake	12 Nov.	10 Dec.	14 Jan.	18 Feb.	19 March	22 April	21 May	17 June	29 July	26 Aug.	1 Oct.
Coelenterata:											
Cordylophora lacustris Allman								+	+	+	+
Nematoda:											
Oncholaimium oxyuris (Ditlevsen)							+	+	+	+	+
Chromadorita leuckarti (DeMan)							+	+	+	+	+
Theristus sp.											
Annelida:											
Nereis diversicolor O. F. Müller						+	+	+	+	+	+
Nais variabilis Piguet							+	+	+	+	+
Crustacea:											
Microarthridion littorale (Poppe)							+	+	+	+	+
Balanus improvisus Darwin										+	+
Sphaeroma hookeri Leach						+	+	+	+	+	+
Jaera albifrons Leach								+			
Gammarus sp. (juv.)							+	+	+		
Gammarus zaddachi salinus Spooner									+	+	+
Corophium sp.									+	+	
Acarina:											
Copidognathus (s.s.) *fabricusi* (Lohmann)											+
Insecta:											
Chironomidae (larvae and pupae)								+	+		
Mollusca:											
Hydrobia jenkinsi, Smith							+	+	+	+	+
Eubranchus exiguus (Alder et Hancock)									+	+	+
Polyzoa:											
Concopeum spiculatum (L.)								+	+	+	+
Bowerbankia gracilis Leidy										+	+
Outfall											
Algae:											
Enteromorpha intestinalis Link						+	+	+	+	+	+
Enteromorpha ahlneriana Bliding						+	+	+	+	+	+

Protozoa:										
Vorticellidae (colonial)					+	+	+	+	+	+
Coelenterata:										
Cordylophora lacustris Allman			+	+	+	+	+	+	+	+
Actinia sp.	+	+								
Nematoda:										
Oncholaimium oxyuris (Ditlevsen)					+	+	+	+	+	+
Chromadorita leuckarti (De Man)					+	+	+	+	+	+
Annelida:										
Nereis diversicolor O. F. Müller						+	+	+	+	+
Nais variabilis Piguet					+	+	+	+	+	+
Crustacea:										
Microarthridion littorale (Poppe)						+	+	+	+	+
Balanus improvisus Darwin										
Sphaeroma hookeri Leach					+	+	+	+	+	+
Jaera sp. (juv.)					+					
Jaera albifrons Leach						+				
Gammarus sp. (juv.)										
Gammarus zaddachi salinus Spooner						+	+	+	+	+
Corophium sp.									+	
Acarina:										
Copidognathus (s.s.) fabriciusi (Lohmann)										
Insecta:										
Chironomidae (larvae and pupae)							+	+		
Mollusca:										
Hydrobia jenkinsi Smith				+		+	+	+	+	+
Eubranchus exiguus (Alder et Hancock)						+				
Mytilus edulis L.	+		+		+	+				
Polyzoa:										
Conopeum spiculatum (L.)			+		+	+	+	+		
Bowerbankia gracilis Leidy									+	
Pisces:										
Anguilla anguilla (L.)						+		+		

young *Nereis diversicolor*. The growth of this Coelenterate in the outfall is also hampered by *Enteromorpha*.

The thick growth of algae in the outfall and the growths of Hydrozoa and Polyzoa in the intake give shelter to other benthonic motile forms. Nematoda and Annelida are very abundant in both places. Among Crustacea the most numerous are *Sphaeroma hookeri* and *Gammarus zaddachi salinus*. *Balanus improvisus* was only found as single specimens, and should be considered as rather rare in these waters*. *Jaera albifrons* and another *Jaera* sp. were also found as single specimens.

Single specimens of *Copidognathus* (*s.s.*) *fabriciusi* were found among the colonies of *Cordylophora lacustris* and *Conopeum spiculatum*. Of the Mollusca, *Hydrobia jenkinsi* occurs in great numbers, but *Eubranchus exiguus* was more abundant on the intake slabs than in the outfall.

Comparing the results given in the two parts of Table 2, the conclusion can be drawn that the appearance of organisms on the slabs takes place much earlier in the outfall than in the intake area. There is no difference, however, in the specific composition of the fauna found, but algae for some reason do not occur in the intake.

DISCUSSION

Though based on one annual cycle only, the results indicate that the outfall area is more favourable than the intake. Though the light regime was the same, no vegetation was observed in the intake, and a prolific growth of algae in the outfall. On the other hand denser animal populations (Coelenterata, Polyzoa) were found in the intake than in the outfall. This could be attributed to the lack of competitors (Algae) and also to the much lower velocity of the water pumped into the station. In both cases, however, the outfall Algae, and the intake Hydrozoa and Polyzoa provided adequate protection for a similar number of species. It is difficult to say whether settlement of the organisms takes place during the operation of the station or in the periods when there is no water movement in the intake and in the outfall.

It should be also remembered that some of the organisms which are pumped into the condensers of the power station are exposed to chlorine and higher temperature, while those which live around the intake are undisturbed by these factors.

In some periods the intake slabs were covered with a coat of slime in which nematodes and annelids were found, but this coat disappeared, probably washed off by the action of waves during heavy storms; this happened in the first months of observation. Once the fixed organisms appeared they persisted up to the end of the observation.

It seems likely that the settling of the initial stages of Algae, Coelenterata Crustacea, Mollusca and Polyzoa takes place when the power station stops operating, and the water is more or less still. These periods are long enough to allow the larval forms to fix themselves to the substratum.

* This species has unexpectedly appeared in large numbers in 1959-60.

Comparing the results obtained in the experimental slabs in the intake and in the outfall area, no ill-effect on the organisms quoted was found. On the contrary, it might be supposed that the outfall area is more beneficial than the intake, probably because of the higher temperature of the water.

ACKNOWLEDGMENTS

Most cordial thanks are expressed to Dr C. Bliding of Kristinebergs Zoological Station, Fiskebäckskol, Sweden, for the identification of the species of Algae, and to Dr G. O. Evans, Dr J. P. Harding, Dr W. J. Rees, Mr J. W. Coles, Miss P. L. Cook, and Mr R. W. Ingle, of the British Museum (Natural History), and to Dr T. Gascoigne for their kind identification of the material collected.

Thanks are also expressed to the Central Electricity Generating Board for permission to publish this paper, and to Mr A. Beckett, the Superintendent of Roosecote Power Station, for his friendly collaboration and assistance, and to Mr H. Brown and Mr L. Tylor, the station chemist; also to Miss E. Evans for the analysis of the water.

SUMMARY

1. A year's observations were made on the settling of benthonic organisms on experimental slabs placed in the intake and in the outfall water of the power station.

2. No growth of Algae was found in the intake, but there was very prolific growth in the outfall.

3. No difference in the specific composition of benthonic invertebrates was found between the intake and the outfall slabs.

4. It is supposed that the outfall area is beneficial in some respect as the benthonic forms appear earlier than in the intake.

5. The general characteristic of the environment, and the factors introduced by the power station into the aquatic medium are given.

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THE NATURAL MORTALITY OF *ERIOISCHIA BRASSICAE* (BOUCHÉ) (DIPT., ANTHOMYIIDAE): LIFE TABLES AND THEIR INTERPRETATION

By R. D. HUGHES and B. MITCHELL

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(With 7 Figures in the Text)

In the light of Morris's recent paper (1957) a preliminary attempt was made by Hughes & Salter (1959) to interpret the available mortality data for the cabbage rootfly (*Erioischia brassicae*). Using the methods described in the latter paper and in Hughes (1959), more accurate life tables have been constructed for six generations of the pest as it occurs at Wellesbourne and these are shown in Table 1. From estimates of the peak numbers of the various instars, the total mortalities were found by difference. Mortalities during the pupal stage were examined in detail by rearing samples of pupae, collected at regular intervals from the field population. The causes of mortality given by Hughes & Salter account for all statistically significant mortality.

INTERPRETATION OF THE LIFE TABLES

The numerical significance of apparent changes in the mean population of individuals on each plant has been examined by calculating the standard error of the estimates wherever this was possible. These calculations lead to the following conclusions.

Within any one generation the numbers of each of the larval instars and the pupal instar were not significantly different from each other and therefore no mortality can be assumed to occur between the first instar and the beginning of the pupal stage. Between the numbers of pupae and of adults emerging from the soil there was always a significant reduction accounted for by parasites and other factors, which can be demonstrated by rearing samples of the pupal population in the insectary. Error terms cannot readily be computed for the indirect estimates of total egg numbers (Hughes 1959) and in only one generation was it possible to obtain two completely independent estimates. However, in this case the standard error of the two totals was only 4% of the mean, so the assumption that the 90% differences between egg and larval numbers were significant throughout is reasonable.

Secondly the numbers of eggs laid in the second generation in each year are probably significantly lower than the numbers laid in the first. Cultures of both insectary and field reared flies have shown that second generation females lay fewer eggs than the somewhat larger individuals of the first generation. The number of eggs laid in the spring of 1959 was significantly greater than in any other generation. Larval numbers in both 1959 generations were significantly

Table 1. *Life tables of the first and second generations of* Erioischia brassicae *at Wellesbourne during the years 1957, 1958 and 1959*

Age interval	Generation 1957a	1957b	1958a	1958b	1959a	1959b
	Peak numbers per plant					
Eggs	405·2	298·1	486·6	310·8	709·5 * 753·7	341·1
Newly hatched larvae						
1st larvae	38·5 ± 6·0	17·3	25·3 ± 3·2	21·8 ± 1·3	64·5 ± 5·0	84·9 ± 8·3
2nd larvae	–	–	25·3 ± 3·2	21·8 ± 1·3	64·4 ± 5·0	84·6 ± 8·3
3rd larvae	–	–	24·0 ± 3·1	21·5 ± 0·8	63·9 ± 5·1	83·1 ± 10·1
Pupae	28·1 ± 6·8	17·0	24·8 ± 1·3	21·5 ± 0·5	63·4 ± 3·9	83·1 ± 10·1
Newly emerged adults	9·8 ± 2·3	9·4	12·7 ± 2·2	14·3 ± 3·0	6·5 ± 2·5	12·5 ± 2·9

Causes of Mortality	Generation 1957a	1957b	1958a	1958b	1959a	1959b
	Percentage mortalities					
(i) Egg losses, predation						
(ii) Reduced viability	90·5	94·2	94·8	93·0	91·2	75·2
(iii) Failure to find host plant						
(iv) Death of host plant						
(v) Other causes, predation	26·9	2·0	2·0	1·4	1·7	2·1
(vi) Parasitized by:						
Idiomorpha rapae	9	22	21	25	20	7
Phygadveon trichops	0·1	0·0	0·2	2·6	1·1	1·3
Aleochara bipustulata	7·9	3·4	0·8	0·0	2·7	23·8
A. bilineata	2·1	9·6	0·2	1·0	0·3	2·6
(vii) Failure of development, caused by death of host plant	44·8	9·7†	25·0	4·8†	32·5	23·7
(viii) Failure to reach soil surface	1·0		3·0		68·5	63·8

* Two independent estimates using method given by Hughes (1959).
† Failure to reach soil surface too small for accurate estimation.

greater than in the earlier years. Only in the spring generation of 1959 was there a significant change in the numbers of emerging adults, between consecutive generations.

Hughes & Salter (1959) gave the larval mortality for three other generations not included in Table 1, and in all cases differences between the numbers of first instar larvae and of pupae were well within the average experimental error of the present observations. This allows the remaining mortality to be divided clearly into prelarval and postlarval sections. The significant prelarval mortality consists almost entirely of predation on the eggs (Hughes 1959) together with a slight reduction of their viability. The postlarval section can be subdivided into a group of important mortalities concurrently affecting the pupal stage, and the only adult mortality measured, failure to reach the soil surface. Only during the prolonged drought of 1959 was this last factor significant.

The mortality data can therefore be initially analysed in terms of three groups of factors. Hughes & Salter used an index of population trend (Balch & Bird 1944) to compare, between generations, the total mortality of each immature stage. The use of this index is equivalent to transforming percentage mortality to survival, expressed as a proportion of the average survival of individuals exposed to a

Table 2. *The range of index of population trends, 1957-9*

Prelarval mortality	0·51-2·43	
Postlarval (i) pupal mortality	0·73-1·38	(*cf.* Hughes & Salter 0·81-1·40)
(ii) early adult mortality	0·48-1·50	

particular mortality factor. Thus the average survival of rootfly eggs is 100— per cent average mortality, *i.e.* 100—89·8 = 10·2. Therefore in the second generation of 1959, when the survival was 24·8%, the index of population trend was 24·8/10·2 = 2·43, or more than twice the normal proportion of eggs hatched. The range of variation seen in the pre- and post-larval mortalities can be analysed in this way (Table 2). Prelarval mortalities caused greater changes in subsequent abundance than postlarval. The importance of the variations of a particular mortality within a contemporary group depends on the proportion of deaths arising from that factor and on the constancy of the contemporary mortality. Thus variations of egg predation were of primary importance in the prelarval group, because the reduced viability of the eggs probably accounted for only 1% of the total mortality and was relatively constant. The importance of variation of particular mortality factors in the postlarval group was more difficult to elucidate because a major increase in one factor was often cancelled by decreases of the others (Table 3). From this table it is clear that interference by other factors robbed parasitism of any regular importance. However, the overall level of parasitism remained remarkably constant, which enhanced the importance of the other mortality in the pupal stage, namely failure of development caused by the death of the host plant.

A major point to be considered in the analysis of the mortality data is the

possibility that one or more of the factors is operating with an intensity of action dependent in some way upon the numbers of individuals present. Such factors are of special importance when they occur in sequence with other variable mortalities, since they tend to counteract any previous population changes. The very small variation of the numbers of emerging adults compared with the numbers of other stages suggests that factors of this type may be operating. All factors causing death of the insects were considered in this role, except purely climatic effects, but only egg predation, larval parasitism by *Idiomorpha rapae* and pupal mortality due to death of the host plant were consistently large enough to measure accurately and consider in detail.

(*a*) *Predation of eggs*

Whilst the numbers of emerging adults did not vary very much, the number of eggs they laid varied for two reasons. Firstly, individual flies of the spring generations were about half as large again as those of the others and laid comparably more eggs. Preliminary observations made on pupae collected from the field and

Table 3. *The interference between contemporary mortality factors expressed as percentages*

Generation	Larval parasitism (*a*)	Contemporary mortality (*b*+*c*)	Pupal parasitism (*b*)	Contemporary mortality (*a*+*c*)	'Other' mortality (*c*)	Contemporary mortality (*a*+*b*)
1957a	9·1	55·2	10·0	54·3	45·2	19·1
1957b	22·0	22·7	13·0	31·7	9·7	35·0
1958a	21·2	27·6	1·0	47·8	26·6	22·2
1958b	27·6	5·9	1·0	32·5	4·8	28·7
1959a	21·1	35·5	3·0	53·6	32·5	24·0
1959b	8·3	51·1	26·4	32·0	23·7	34·7

reared in an insectary suggested that about 11 mg was the normal weight of female flies in the summer while those of the spring generation averaged around 16 mg. The relative number of eggs produced were respectively 40-60 as compared with 60-80. Secondly, mortality before the completion of oviposition can reduce the numbers of eggs laid. In this case the role of the weather in stimulating early oviposition can be very important. In the first generation in 1959 it was observed that almost all the eggs were laid in the first 10 days of a long period of suitable weather (Fig. 1). If egg numbers fluctuate from generation to generation does the intensity of predation vary in such a way as to counteract these population changes?

The complex of factors affecting egg predation is broadly understood and an analogue of the factors and interactions is shown diagrammatically in Fig. 2 as a system of wheels and continuous belts. Each wheel represents a factor in the system and a turn in the direction indicated by the arrow represents an increase of the factor concerned. Touching wheels and the continuous belts indicate correlations between factors. The wheels are not drawn to scale and the efficiency

of any wheel in driving other parts of the system must be thought of as varying with circumstances such that an equilibrium position of all the parts will be reached for any particular combination of circumstances. The analogue illustrates the manner in which egg mortality is affected directly by three known factors: Predator activities, the mean temperature of the eggs, and rainfall. These factors in their turn are affected by many others, of which only the most important are considered.

The proportion of eggs eaten is a direct function of predator activities. This term is used to emphasize the duality of predation, the effectiveness of the beetles being governed partly by their abundance and partly by their activity which is correlated with soil surface temperatures (Mitchell 1959), an increase in temperature leading to greater beetle activity and so to more eggs being eaten.

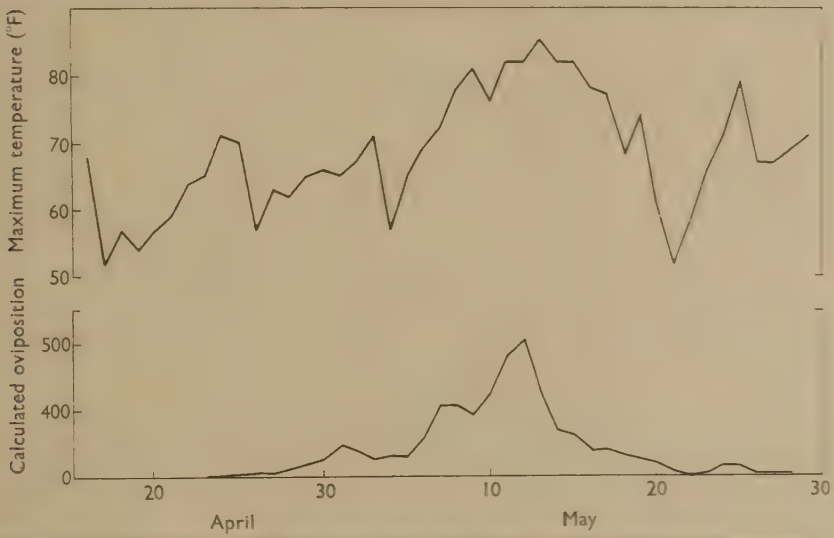

Fig. 1. Variation of daily oviposition under each plant with the daily maximum temperature.

The proportion of eggs eaten before they hatch is also a direct function of the incubation period which in turn is inversely proportional to the mean temperature of the eggs. The mean temperature of the eggs is very similar to that of the soil surface around the base of the plant where they are laid. Increasing temperature gives a shorter incubation period so that fewer eggs are eaten.

The proportion of eggs eaten is reduced by rainfall, especially by heavy showers which tend to wash the eggs down into the soil interstices and seal them from further predation (Hughes 1959). Rain causes lower temperatures and so less predator activity with the result that fewer eggs are eaten; heavy rain seals eggs into the soil so that again fewer eggs are eaten.

Soil surface temperatures control the opposing effects of beetle activity and incubation period upon the proportion of eggs eaten. The summation of these

effects, therefore, finally depends on the difference between the soil surface temperatures between and below the plants, a difference that varies with the growth of the crop. For any given crop the relationship between temperatures between and under the plants gives rise to a direct correlation between the daily catches of beetles and the rate at which the eggs develop on that day. The survival of eggs is related to the daily beetle catches by the expression $B\alpha \log q$, where q is the daily survival of eggs (Hughes 1959), and since the incubation period is the

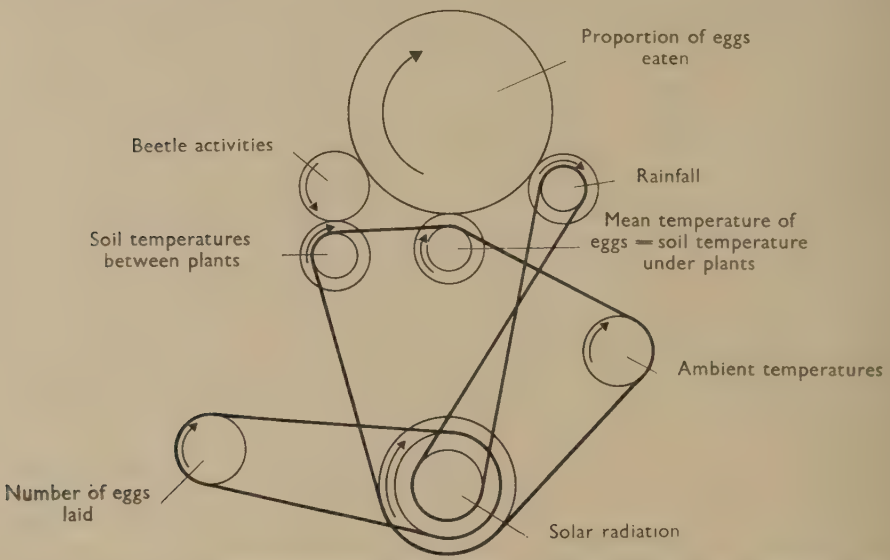

Fig. 2. Analogue of the interrelationships controlling the predation of rootfly eggs by beetles. For full explanation see text. Arrows on wheels indicate that a turn in that direction denotes an increase of the factor concerned.

reciprocal of the daily rate of development, there is a derived relationship $\log q \alpha 1/p$ (where p is the incubation period) which gives rise to changes in overall survival of the eggs with temperature of the type seen in Fig. 3. Above the threshhold of development of the eggs the shorter incubation periods allow more eggs to escape although predation increases with temperature. Thus eggs laid during hot weather, as in the spring of 1959, are more likely to survive. However, as more eggs are laid each day in hot weather this brings the discussion back to the possibility that predation becomes more intense in the presence of large numbers of eggs. As there had been indirect evidence of a numerical increase in the predator population of the cabbage plot during the first generation of 1958, the simplest hypothesis, that the beetle activities were related to the number of eggs present, was tested experimentally during the spring of 1959.

To demonstrate such a build up of the activities of predators, measurements must be made before, during and after the oviposition period of the cabbage

rootfly. Also accurate counts of the number of eggs around each plant are necessary for comparison with any beetle population changes. Beetle activities were followed by a pit-trapping technique using 1 lb jam-jars sunk flush with the soil surface (Mitchell 1959). These traps were emptied daily between 11.15 and 12.15 h, using a portable electric suction apparatus (Johnson, Southwood & Entwhistle 1955). The daily trap catches measured the population density modified by the average activity of individual beetles, which in turn varied with the prevailing weather. During this experiment the predator population consisted almost entirely of *Bembidion lampros* Herbst (Coleoptera, Carabidae), and other predator species (less than 5% of the total catch) were ignored.

Mitchell (1959) has made observations on *B. lampros*, describing behavioural mechanisms which could cause an increase of predator activities. The beetle is

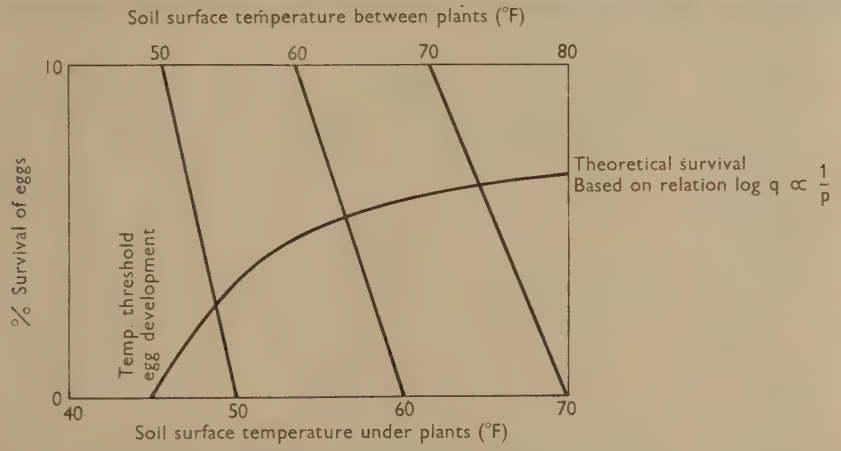

Fig. 3. The relationship between the overall survival of eggs and soil temperatures. The overall survival is the equilibrium point between daily egg survival and the incubation period of the eggs. The relation between temperatures under and between the plants is taken from data obtained from the first summer cabbage crop of 1959.

very mobile and is not confined to the area of the experimental crop. Beetles on this area form a very small proportion of a much larger population and because of their mobility there is a very rapid turnover of the individuals occurring on any experimental area. Population movements have been studied by trapping the beetles, which combined with mark and recapture techniques has shown that changeover rates into and out of the 3000 sq. ft experimental plots can exceed 40% per day. Under these circumstances of rapid immigration and emigration any reduction of the emigration rate on the experimental plots will be reflected in a build up of the beetle population in the area concerned. Now *B. lampros* is known to move more or less directly across open cultivated soil, but this behaviour changes after finding and eating food, when for several seconds the beetle circles in the immediate vicinity before resuming direct progression. It is suggested that on an area containing a relatively common source of food there would be an

increase of the number of turning movements and of the time that individual beetles were at rest, thus increasing the amount of searching and reducing the emigration rate. In this way the presence of large numbers of rootfly eggs could cause a kinetic aggregation of the beetle population and so increase the proportion of eggs eaten.

To separate any unique changes occurring on the cabbage plot, a comparison was made of the trap catches made on it and on an adjacent plot of bare ground, similar in size (30 × 100 ft) and having a similar soil structure. By a daily comparison of the catches in ninety traps on each plot (three rows of thirty, rows 10 ft apart, traps 3·5 ft apart) it was possible to see which changes in the catch were common to both plots as a result of similar weather effects or overall population changes. The significant differences between the plot catches reflected changes

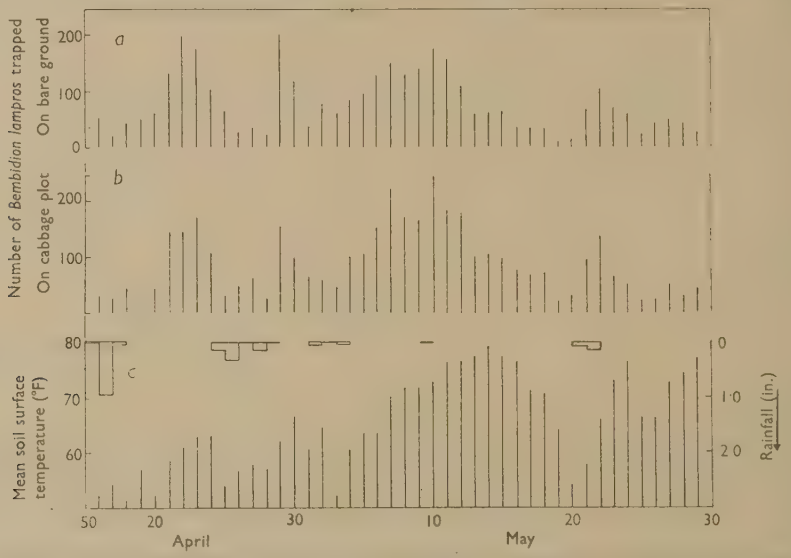

Fig. 4. Comparison of beetle trap catches on bare ground and cabbage plot, with weather conditions.

resulting from the effects of the cabbage crop and at the appropriate time, of the presence of the cabbage rootfly eggs. As there was no heavy rainfall to seal the eggs into the soil during the period when most eggs were laid, a good estimate of the number of eggs available to the beetles could be obtained by taking soil samples daily from around nine randomly selected plants and counting the number of eggs present. This figure was taken as an index of the egg population density on each day (see Fig. 5b). Fig. 4 shows the catches on the two plots over a period of 45 days during the spring of 1959. The variations of two climatic factors, soil-surface temperature on bare ground and rainfall, are given for comparison. High catches occurred on hot days on both plots and similarly low catches coincided with cold or wet days. Clearly the beetles on both plots were responding to weather conditions in the same way.

When the relative differences between each days catch on the two plots were considered, a new and simpler pattern emerged (Fig. 5). The differences are expressed in terms of the proportion of the total catch on both plots which was found on the cabbage plot. For the first 3 weeks about 50% of the beetles were caught on the cabbage plot and any differences were not consistently significant. Then from about 5 May there was a steady increase of the proportion of the total catch taken from the cabbage crop, which lasted for about 2 weeks. Thereafter the proportion falls off again to more or less equal numbers on the two plots.

In interpreting these data, the effects of both the cabbage crop and the rootfly eggs must be considered. Mitchell (1959) has shown that the numbers of *B. lampros* among a crop is inversely related to the amount of plant cover. As the cabbage crop was growing steadily during the period of the experiment, this effect would be reflected in a steady downward trend in the beetle catches on the cabbage

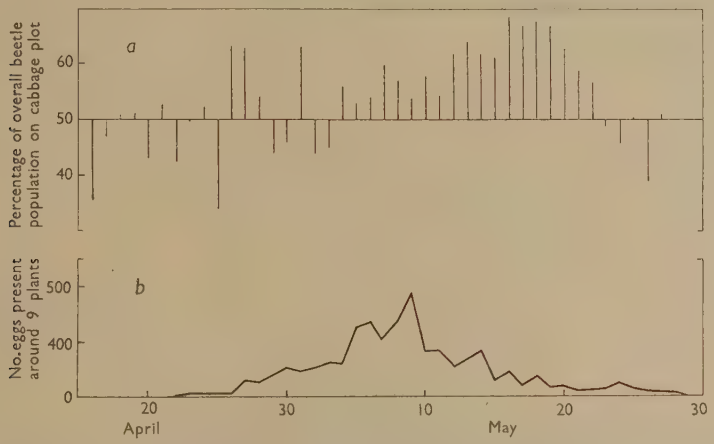

Fig. 5. Comparison of the population of the overall catch of *Bembidion lampros* trapped on the cabbage plot with the number of rootfly eggs present around each cabbage plant.

crop. No such trend is apparent in Fig. 4a. The possibility that the beetles were using the crop as shade during the hot sunny oviposition period cannot be ignored entirely, but, this would be a complete reversal of their normal behaviour. There was not a similar hot period in 1958 when, as mentioned above, beetle numbers probably also increased. When the proportion of beetles on the cabbage plot is compared with the egg numbers (Fig. 5), it can be seen that whilst both populations have a well defined peak, that of the egg numbers occurs about a week earlier than that of the beetle numbers. However, the egg density at the time of the beetle peak (18 May) was between 150 and 200, which compares well with the number of eggs present at the start of the build up of beetle numbers. Although there was an increase of beetle activity, a glance at the life table for the first generation of 1959 shows that there was no corresponding increase of the predation mortality. This mortality actually fell compared with the generations of the

previous year, probably as a result of average soil temperatures being some 10° higher than in the 1958 season (see Fig. 3).

(*b*) *Parasitism of larvae by* Idiomorpha rapae

Milne quoted by Andrewartha & Birch 1954) has pointed out some of the difficulties of demonstrating the existence of a relationship between percentage parasitism and host density in field data of the type given in Table 1. However, the existence of a behavioural mechanism altering the searching pattern of the parasite when it has contacted one host so that it will more readily find other hosts in the near vicinity, would be strong circumstantial evidence for such a relationship, and this should show up during field sampling. There should be a within-sample variation in parasitism related to the host density within the samples. Observations made on a rootfly population attacking a swede crop in

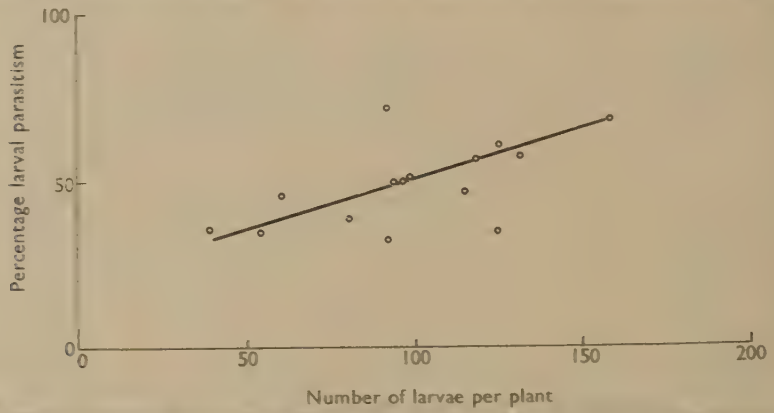

Fig. 6. The relationship between the within-sample variation of larval numbers and the percentage parasitism by *Idiomorpha rapae*.

1958 are summarized in Fig. 6. The apparent relationship is not significant but indicates that further observations might confirm its existence. However, the rate of parasitism only doubled over a four-fold increase of host density, which makes it unlikely that this mechanism can have any important stabilizing effect on population numbers at the levels concerned, especially when the interference of contemporary mortality is considered.

(*c*) *Pupal mortality caused by the death of the host plant*

When the numbers of insects get too large they impair or destroy their own food supply and higher mortality results from the subsequent starvation of the population. In the case of the feeding larvae of *E. brassicae* no direct mortality seems to occur, but the malnutrition results later in the incomplete development of some of the pupae so that adults do not emerge. The cabbage rootfly larvae feed primarily on the root cortex of the host plant, and the area of cortex damaged

was found to be proportional to the number of insects feeding. This type of damage reduces the amount of the water absorbing tissue and the plants respond as if to water shortage, first wilting, then becoming discoloured and stunted, and finally often dying. The proportion of dead and severely stunted plants was found by experiment in 1959 to be directly related to the number of larvae attacking the crop (Fig. 6), so there was no doubt that the insects were limiting their own food supply. The relationship between the mortality of the plants and the insect population on the crop is probably of the type $M = k(N-a)$, the host plants being able to survive when the number of rootfly attacking the root system falls below a certain value a, which will vary from crop to crop as shown below. In the six generations studied, incomplete pupal development varied from a few to nearly 50% of the individuals. In this mortality occasioned by the self limitation of the food supply there is a potentially accurate mechanism for preventing large changes in the insect population, especially as there is little interference by contemporary mortality factors (see above). When, however, the percentage mortality is compared with the number of larvae attacking the crop there is no clear relationship (Table 4).

Table 4. *The relationship between pupal mortality caused by the death of host plants and the peak number of larvae attacking the crop*

	Generation					
	1957a	1957b	1958a	1958b	1959a	1959b
Peak number of larvae	38·5	17·3	25·3	21·8	64·5	84·9
Plants killed (%)	34	–	1	4	42	8
Pupae failed to develop (%)	44·8	9·7*	25·0	4·8*	32·5	23·7

* Unseparated (see Table 1).

Climatic and other factors had affected the relationship by changing the ability of the host plant to survive the damage caused by the larvae. Thus, in prolonged hot dry weather a density of about thirty larvae per plant can kill a large proportion of the crop whereas in a cool wet season the same number of insects would fail to cause noticeable losses. Soil types are complementary to the weather; for example, host plants growing in soils which dry out quickly will be killed by fewer insects than plants grown on moisture retaining soils. Similarly the size and the rate of growth of the host plant during the period of severe attack by large third stage larvae will change its chances of survival. Older plants need more insects to kill them and may even survive long enough to allow the insects to complete their development successfully. The 1959 generations are cases in point, where large numbers of larvae were present but the plants were large enough to support them until their development was nearly completed.

The interaction of the host plant, weather and soil modifies the slope and the position of the curve in Fig. 7. Although on any one crop the mortality rate of the pupae will always be related to their population density, the variation of the

parameters of the relationship with weather etc. may cause the mortality to be too high or too low to counteract precisely any prior population changes.

CO-ORDINATION BY THE WEATHER

So far there is no unequivocal evidence of any particular factor acting consistently each year to stabilize rootfly numbers in Long Meadow. Yet in nine generations studied in detail by the present authors and in six generations where

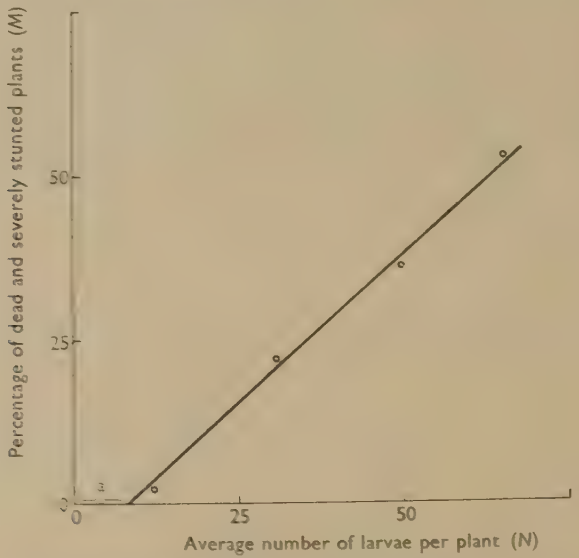

Fig. 7. Typical relationship between the proportion of dead plants and the number of rootfly larvae per plant. Experimental data from Wright, Hughes & Worrall (1960).

estimates of root damage have been made (Wright, personal communication), there has been no evidence of a major variation in the infestations of this pest, over a period totalling 6 years. Differences in crop damage have been primarily manifestations of the weather in particular seasons. On the evidence of the six life tables given above, when any unusual number of individuals occurred sooner or later the change was counteracted effectively by a later mortality in that generation. If the factors concerned operated randomly one would expect rootfly numbers to vary much more than has been observed in the field.

An overall consideration of the modifications to the mortalities caused by the weather leads to the conclusion that conditions favouring the survival of particular stages of the life cycle will, if the weather continues the same, often favour a subsequent mortality. As rootfly generations are relatively short and the immature stages overlap strongly, a single weather pattern will often govern the modifications of many of the mortality factors.

The weather at the time of year when rootfly generations occur is seldom extreme and can be classified in terms of more or less warm and inversely less or more wet. The range of weather is set out in the first two columns of Table 5. In the next four columns are given the usual modifications of mortality factors at points in the range represented by the major parts of the particular generations indicated in the last column. It must be pointed out that other factors have also modified certain of the life tables so that a direct correspondence between Tables 1 and 5 must not be expected. The interesting thing about the sequences of modifications is the way they are balanced; particularly strong mortalities are followed by general favouring of survival and *vice versa*. There is clearly the

Table 5. *The linkage of mortality modifications into balanced sequences by particular weather patterns*

Weather		Modification of mortalities				Example generation
		Reduction of oviposition	Predation of eggs	Failure of pupal development	Failure of adults to reach the soil surface	
Hot	Trace rain	− − −	+	++	+++	1959a
						1959b
Warm	Trace rain	− −	+++	++	− − −	1958a
	Occasional rain	− −	++	++	− − −	1957a
	Rain often	+	++	− − −	− − −	1958b
Cooler	Heavy rain often	+++	−	−	− − −	1957b

possibility that such balanced sequences could exert a distinct stabilizing effect on the population.

DISCUSSION

The following general conclusions on the importance of particular mortalities can be drawn from their levels, their variabilities, their contemporary mortalities, and the relationship of their intensity of action to the population density.

(*a*) A generally high level of egg predation, which showed one considerable variation in intensity, caused the greatest change in abundance within a single generation. On the whole, however, the level of this mortality was extraordinarily constant around 90 to 95%.

(*b*) The same can be said of the failure of the adults to reach the soil surface. The normal level of this mortality was probably very low, and only in an exceptional year (1959) did it definitely occur and then at a very high level. A possible link between this mortality and the malnutrition of the larvae has been suggested, but there is no clear relationship to the mortality in the pupal stage resulting from this cause (Table 1). Admittedly the drought conditions after spring rain were needed to get the soil into the brick-like state seen in 1959. However, the relationship between these two mortalities in the two generations in that year still is not consistent with the hypothesis; especially as the ground was cultivated between generations thus breaking up the main 'cap'.

(c) Pupal mortality caused by the malnutrition of the larvae emerges as a consistently variable mortality with a normal level sufficient to cause substantial change of abundance which are obvious because of the low interference by its contemporary factors.

Little evidence of specific population regulating factors has been found even though the numbers of rootflies remain amazingly stable over the years. The observations seem to support Milne's (1957) view of the imperfections of certain density dependent factors, such as those natural enemies which have a density stabilizing tendency. Milne continues by citing intraspecific competition for food as the only mortality factor infallibly preventing the increase of the population beyond the limit of the resources available. No close approach to the upper limit of population size has yet been observed, but at the population levels recorded this factor's influence was substantially modified by the weather, etc.

The most important feature of the stabilization of numbers to be seen in the life tables of the Long Meadow population of *Erioischia brassicae* is that when any change in abundance occurred it was counteracted before the end of the same generation. This indicates a co-ordination of the mortalities within a generation, which in the absence of precise linkages to the baseline of population density has led to the suggested alternative of co-ordination by the physical environment.

SUMMARY

1. Life tables have been constructed for six generations of the cabbage rootfly as it occurs in one field at Wellesbourne.

2. The importance of particular causes of death are discussed in relation to the life tables.

3. Whilst rootfly populations have remained remarkably constant over the years, no particular factor seems to be concerned in this regulation.

4. Varying combinations of all factors, possibly sequentially modified by weather conditions, seem to cope with any potential increase or decrease in numbers before the end of the generation in which the change occurs.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge our debt to Dorothy D. Salter who carried out much of the routine work which forms the basis of this study.

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ADDENDUM

By R. D. HUGHES

No mortality factor appears adequate for the precise numerical adjustment of the population of adult *E. brassicae* between generations. Furthermore, co-ordination of several mortalities by the weather still could not account for the stability observed. After discussions with colleagues at C.S.I.R.O., Canberra, the problem has been reconsidered.

The life-tables have been constructed only for the fly populations on crops of one variety of cabbage, grown in various parts of the same field. The populations therefore were probably genetically similar and fed on uniform crops which varied primarily with the prevailing weather. Under these conditions a very constant mean number of adult flies was produced from each plant. Although the numbers produced from cauliflowers grown in the same field are higher than on cabbage they show similar stability from generation to generation.

The substantial differences of oviposition and survival of the eggs would be expected to induce equivalent fluctuations in the adult population. Differences in oviposition arise from variations in fertility and in the survival of egg laying females. Once laid the egg survival in the presence of efficient predators depends largely on the vagaries of the weather and the numbers of feeding larvae have shown at least four-fold variation.

Only the direct relationship between the numbers of feeding larvae and the proportion of plants killed seems to have the necessary precision to account for the accurate numerical regulation. Each larva must have caused a change in the biochemistry of its host plant which, in conjunction with certain weather conditions, resulted in failure to replace the water-absorbing tissue eaten. Thus the insects were limiting their food supply in proportion to the numbers feeding.

Nearly all larvae pupate and, unless some of the host plants have been killed, the great majority of pupae formed will complete their development. At this stage there is still a surplus of individuals, which if they survived would, on average, cause a threefold increase of the population in each generation.

However, when host plants are killed a large proportion of pupae will sometimes fail to develop further, probably as the result of inadequate larval food.

Extending this idea there would seem to be a minimum diet necessary to ensure the survival of an individual. The surplus of individuals, which have had an inadequate larval diet, are vulnerable to any stress which may be subsequently imposed, e.g. eclosion, emergence of adults through dry, compacted soil, and climatic extremes during the preoviposition period. The order and relative intensities of the stresses will determine which will kill the majority of the surplus individuals.

Parasitism of either larvae or pupae cannot be part of this mechanism of regulation and must be regarded as disturbing factors accounting for some of the slight variation of adult numbers observed.

A STUDY OF THE RELATIONS BETWEEN ROE, RED AND FALLOW DEER, WITH SPECIAL REFERENCE TO DRUMMOND HILL FOREST, SCOTLAND

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(With Plate 8 and 2 Figures in the Text)

Correspondence has appeared in the literature concerning the relationships between red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and some other species, such as Japanese deer (*Cervus nippon*), which are feral in the British Isles. Competition, described as antipathy or antagonism by various writers, appears to be the most widely accepted mechanism whereby relative abundance of one deer species is often correlated with relative scarcity of others. Other explanations involve geographical limits of distribution, two examples being the relative abundance of fallow deer in the south of England, and of roe deer in the Lake District (Delap 1955, Carne 1955).

Carne (1954) has stated that Japanese (syn. sika) and fallow deer are, having been introduced into Britain, a powerful deterrent to the roe; he claims support for this contention from historical records which he considers show that as fallow deer have increased in an area, roe deer have decreased, often to extinction. Having observed in the Lake District of England that fallow deer have never established themselves in forests occupied by roe deer, Carne confirmed (1955) a statement by Delap (1955) that there is antipathy between them. Delap also stated that roe deer and red deer or red deer and fallow deer can 'associate happily', but that antagonism exists between roe deer and fallow deer. However, even co-existence of red deer and roe deer does not appear to be a constant feature; Wildash (1951) records that roe deer are seldom found where red deer are present in any numbers in Austria, that the red deer is a 'natural enemy' of the roe, and also that Austrian foresters could not give any reason for this antipathy.

The purpose of this paper is to examine these ideas in the light of further evidence. It will be shown that roe, red and fallow deer are characteristically most numerous at different stages in the development of several British forests; when two or more of these three species are present in the same forest area, the number of each of them increases and decreases in a successional manner, which is related to development of the forest habitat towards a climax of mature trees. Such successional changes of the deer fauna are considered to be similar in nature to the marked changes which were shown to occur to the species composition of the bird fauna when a heathland area in East Anglia was afforested (Lack & Lack 1951).

* This paper represents part of the work undertaken as a thesis for the Honours School of Forestry while I was a New Zealand Forest Service Bursar at the University of Oxford.

METHODS

The development of the deer herd in Drummond Hill Forest, Central Perthshire, Scotland, was deduced from the game records of the Forestry Commission. The changes of numbers of red, roe and fallow deer were tested (mean square successive difference test, Hald 1952) against the hypothesis that each year's kill could have been drawn as a random sample from a population without trend.

The relationships between the changes of proportion of the deer species and development of the forest were investigated during the spring of 1957 by a study of the distribution of their faecal pellet groups, each of which represents a single defecation, in the various types of forest habitat. Counts were made of the faecal pellet groups (for identification of these see Eberle 1938, Riney 1957, Taylor-Page 1958, Brandt 1908) on thirteen 4-ft-wide belt transects marked on a map of the forest without reference or bias as to the location of types of forest, roads, rides or other features. The location of these transects is shown in Fig. 2; they totalled about $13\frac{1}{4}$ miles in length and 6·23 acres in extent.

The lines were followed as precisely as possible in the field by using a wrist-type, oil bath compass. The 4-ft transect was made up of a strip extending 2 ft to each side of the compass line, and was measured in the field by a knotted cord held out from the centre of the line of march. Pellet groups were considered to be within the transect if more than one-half of them were less than 2 ft from the line of march, and faeces dropped by a moving animal were taken to be within the sample if they occurred in a line right across the transect. Pellet groups were totalled for every 20 yd of the transects (distance measured by pacing) and, at the beginning of each 20 yd, a record was made of the median diameter at breast height (median d.b.h.) of the trees, the tree species, and of the dominant components of the field layer (recorded as grasses, mosses, heather, etc.). This procedure made it possible to draw a map to show the distribution of the deer, and to relate this to the various types of forest habitat. For the distribution map, the pellet counts were pooled in successive groups of five and the densities (per 1200 sq. ft approximately) recorded in this way were plotted on a map of the forest. Pellet group 'contour' maps were drawn from these data.

THE SURVEY

(*a*) *The development of Drummond Hill Forest*

Drummond Hill Forest was first established by Sir Duncan Campbell between 1583 and 1631 (Gillies 1938). It was acquired by the State in 1922 and at that time was fairly completely but irregularly stocked with trees, and many of the stands were overmature (Murray 1935). Most of these overmature stands were cleared for replanting over the following few years though some of the better ones, consisting of beech (*Fagus sylvatica*), oak (*Quercus* sp.) Norway spruce (*Picea abies*) and Sitka spruce (*P. sitchensis*), situated at the eastern end of the hill, were retained. Replanting was mostly completed by 1939. European larch (*Larix decidua*) is the most extensively planted species in the forest, and is confined to the

lower slopes; Scots pine (*Pinus sylvestris*) is the major species of the upper slopes. Douglas fir (*Pseudotsuga taxifolia*), Norway spruce and Sitka spruce, Western hemlock (*Tsuga heterophylla*), Japanese larch (*Larix leptolepis*) and hybrid larch (*L. decidua* × *L. leptolepis*), silver fir (*Abies alba*), ash (*Fraxinus excelsior*) and chestnut (*Castanea sativa*) have been planted in pure stand form or as mixtures.

The forest has passed through three major phases of development since 1922. The establishment phase (1922-39) has been followed by a thicket phase accompanied by first thinnings (1949-50). Most of the stands on the lower slopes have been thinned for the second time since 1950, but stands on the upper slopes are still poorly developed and untreated. The third phase is thus of both well developed pole stands and poor thicket stands.

(*b*) *The development of the deer herd*

The deer present in 1922 were considered by the Forestry Commission to be causing excessive damage to the young forest crops. An attempt was therefore made to exterminate the roe deer, and the red deer herd was reduced to about ten hinds. Only a few fallow deer were present in the forest at that time (Mr A. MacDougall, Forestry Commission stalker, personal communication). The pattern of growth of the deer population is shown in Fig. 1. It is apparent from analysis of the game records that roe deer increased from relatively low numbers during the early 1930s to a peak in the early 1940s and have since declined (significance of trend: $P > 0{\cdot}02$); secondly red deer have increased fairly steadily since the 1930s ($P > 0{\cdot}01$); thirdly there is no evidence from this analysis that the number of fallow deer has changed since 1931 ($P = 0{\cdot}62$), but the game records show an average kill of 2·7 per year during the period before 1944, whereas 5·6 per year have been killed since 1945. Although this suggests that some increase of numbers has occurred, any such change is too small to be demonstrated by the statistical methods used.

The population of roe deer is thought to have decreased during the period 1945-53 as is indicated by the line A-B (Fig. 1). This correction is considered necessary because it was found that the records of roe deer killed since 1945 on two adjacent forest blocks (Tirene and Borland's) have been included with those of animals killed on Drummond Hill. Only two roe deer were killed on Drummond Hill during the forest year 1956-7 (a total of twenty-nine were killed on Drummond Hill, Tirene and Borland's combined). No similar correction is necessary in the case of either fallow or red deer, since fallow deer are absent from both Tirene and Borlands, and there are only a few red deer.

(*c*) *The present distribution of the deer population in Drummond Hill Forest*

The distribution of the three species is shown in Fig. 2. Relationships between this distribution and occurrence of the different types of habitat available to the animals are summarized in Tables 1 and 2, and illustrated in Plate 8.

The pellet group counts for roe deer (Fig. 2) show that this species is restricted,

in small numbers, to the lower slopes of the forest. These areas are clothed largely by European larch of moderate or poor quality and a field layer of sedges, grasses, bracken and moss. Analysis of the proportion of pellet groups of all species in the three field layer types of the forest—(*a*) leaf litter and mosses, (*b*) grasses, sedges and bracken, and (*c*) heather—confirmed that compared with red and

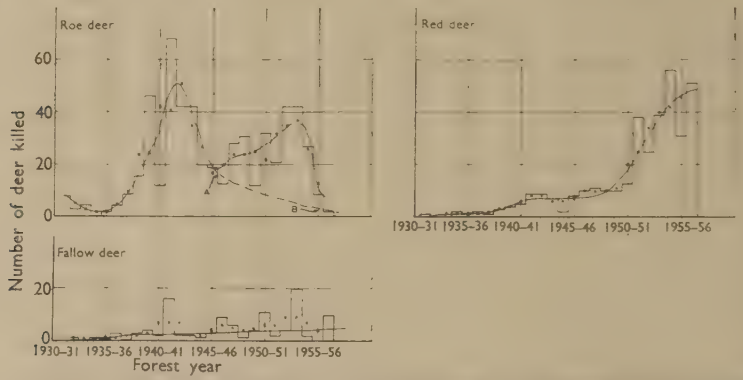

Fig. 1. Histograms and free-hand trend lines of the kill of deer at Drummond Hill Forest during the period 1930-56. The trend line of the kills of roe and red deer are based on running averages of the kill obtained in each successive 3-year period.

fallow deer, roe deer faeces were most dense in those areas with grasses, sedges and bracken ($P > 0{\cdot}01$), and least dense in the heather areas. No correlation was found (at $P = 0{\cdot}05$) between occurrence of roe deer faeces and bole size of the forest stands. A typical example of the kind of habitat occupied by roe deer is shown in Plate 8*A*.

Table 1. *Comparison of proportions of pellet groups counted in each of the three field layer types of the forest, to show distribution of the three deer species*

	Pellet groups observed			%			χ^2		
	Roe	Red	Fallow	Roe	Red	Fallow	Roe	Red	Fallow
Leaf litter and mosses	36	467	20	7	89	4	8·74*	*0·00*	*4·68*
Grasses and/or bracken	60	716	88	7	83	10	15·13**	*4·36*	22·59**
Heather	13	1126	51	1	95	4	*27·65***	3·35	*6·83*

*, significant at 10% level.
**, significant at 1% level.
χ^2 values in italics, observed counts less than expected.

The highest counts of red deer pellet groups were recorded on or near the top of the hill (Fig. 2); they were more dense than average in the heather areas (but the difference from average is not significant at $P = 0{\cdot}10$, Table 1). In all parts of the forest red deer pellets were significantly more dense in stands of smaller trees (less than about 6 in. median d.b.h.), and much less dense in the stands of larger diameter (Table 2). The highest counts were recorded in areas such as that

B

A

C

A. An example of the poor, open European larch stands of the lower northern slopes which are used by roe deer.

B. The photograph was taken from the top of Drummond Hill, looking towards the north east. It is typical of the areas most used by red deer. The heather and stunted Scots pine in the foreground are typical of the areas favoured by red deer (compare with Fig. 2), and the better stands of the lower slopes can be seen in the background.

C. A stand of European larch at the eastern end of Drummond Hill Forest. In a warm site and with a comparatively rich ground flora, it is characteristic of the areas where most fallow deer faeces were recorded.

(*Facing p. 378*)

Table 2. *Analysis by χ^2 of the occurrence of faecal pellet groups*

The habitat types are classified by the dominant field layer and median diameter at breast height of the trees.

		Number of pace groups	Roe deer			Red deer			Fallow deer		
			Pellet groups		χ^2	Pellet groups		χ^2	Pellet groups		χ^2
			Observed	Expected		Observed	Expected		Observed	Expected	
Leaf litter and mosses	10-15 in.	44	0	4·655	*4·6*	21	60·412	*25·7*	2	2·58	*0·1*
	7- 9 in.	69	11	7·300	1·8	65	94·737	*9·3*	7	4·06	2·1
	4- 6 in.	136	15	14·388	0·0	181	186·728	0·2	8	7·99	*0·0*
	1- 3 in.	71	8	7·511	0·0	187	97·483	82·2	2	4·17	*1·1*
	Open ground	20	2	2·116	*0·0*	13	27·460	*7·6*	1	1·17	*0·0*
		340	36		6·4 n.s.	467		125·0**	20		3·3 n.s.
Grasses, sedges and bracken	13-16 in.	18	3	1·935	0·6	16	23·094	*2·2*	1	2·838	*1·2*
	10-12 in.	71	8	7·632	0·0	30	91·093	*40·9*	34	11·196	46·4
	7- 9 in.	194	30	20·855	4·0	177	248·902	*20·7*	26	30·593	*0·7*
	4- 6 in.	222	12	23·865	*5·9*	384	284·826	34·5	18	35·009	*8·3*
	1- 3 in.	10	1	1·075	*0·0*	34	12·830	34·9	0	1·577	*1·6*
	Open ground	43	6	4·622	0·4	75	55·169	7·1	9	6·781	0·7
		558	60		10·9*	716		140·3**	88		58·9**
Heather	5- 6 in.	46	6	3·131	2·6	207	270·9	*15·1*	19	12·282	3·7
	3- 4 in.	71	4	4·832	*0·1*	278	418·2	*46·9*	25	18·957	1·9
	1- 2 in.	20	1	1·361	*0·1*	210	117·8	72·2	2	5·340	*2·1*
	Open ground	54	2	3·675	*0·8*	431	318·1	40·1	5	14·418	*6·2*
		191	13		3·6 n.s.	1126		174·3**	51		13·9**

n.s., not significant.
*, significant at 10% level or better.
**, significant at 1% level or better.
χ^2 values in italics, observed counts less than expected.

shown in Plate 8*B*, and particularly near the dense stands of 30-40 ft high Norway or Sitka spruce which had also water, wallow holes, and open heather in close proximity. The use made of the forest by red deer was progressively less towards lower altitudes and towards the eastern end of the forest.

Fallow deer faeces were, compared with roe and red deer, significantly concentrated in those parts of the forest with a field layer of grasses, etc. (Table 1), and in all parts of the forest they were relatively more abundant than red deer faeces in stands of larger median diameter. The highest counts were recorded in the stands of 10-12 in. median d.b.h. with a field layer of grasses. Such stands are restricted to the two ends of the forest; they are all on the lower slopes of the hill, and the outstanding impression one gains of them is the almost park-like

Fig. 2. The distribution of faecal pellet groups of the three deer species in the forest. The 'contour' maps of pellet group densities are based on the thirteen sample transects. The forest is an isolated whale-back ridge: roe deer are confined to the lower slopes, red deer are most concentrated on the higher slopes and hill top, and the main concentration of fallow deer occurs at the eastern end.

appearance (Plate 8*C*) generally with a heavy sward of grasses underfoot. The forest stands between the group of fallow deer at the eastern end of the forest and that at the western end are younger, typically more dense, and on steeper ground. The Forester, Mr J. Kennedy, reported his impression (private communication) that the fallow deer are becoming more widespread in the forest, tending to spread through the intervening stands between the two groups as they are thinned and brashed, and developing the characteristic open, grassy features of the older stands.

DISCUSSION

The analysis of the Drummond Hill game records indicates that roe deer

increased rapidly during the late 1930s and early 1940s and have since decreased. Red deer have increased at a lower rate and are now more numerous than either roe or fallow deer. It is also apparent that these changes are related to the main phases of development of the forest, which have been earlier described. Exceptional kills of roe deer were obtained towards and shortly after the completion of the establishment phase (until the early 1940s). Increase of red deer has been most marked since the 'thicket with first thinnings phase' (1940-50). Fallow deer have not yet shown marked increase of numbers.

The possibility that this pattern of kills is independent of the population trend must be considered. Disproportionately high kills in any year, for example, can be quite independent of the general population trend and entirely due to intensified or relaxed hunting effort. In such an area as Drummond Hill, however, which has been continuously managed by the Forestry Commission and hunted by the same man for the past 35 years, it is thought that the kills recorded during any period of years are indicative of the number of animals present although the relationship is not necessarily a direct one.

The deduction that there is developing at Drummond Hill Forest a pattern of succession from roe deer, to red deer and eventually to fallow deer, is based for the latter two species upon the study of the distribution of their faecal pellet groups in the different sized tree stands. Red deer pellets were concentrated in the forest stands of smaller diameter than those in which fallow deer pellets were concentrated (Table 2). This suggests that fallow deer will become more widespread and more numerous in the forest when stands of larger diameter form a higher proportion of the entire forest through continued growth.

The finding that roe deer faeces were less numerous than average in the stands of smaller diameter was not expected from the succession hypothesis. Whether their present distribution is due to antipathy towards other species, or to altitude, vegetation, or proximity to the margin of the forest is not clear, but the decrease in their numbers during the past 15 or more years suggests that the species is a 'relic' in a habitat which is now either unfavourable to it, or more favourable for red and fallow deer. The latter explanation seems to be the most probable one because in the two forest blocks adjacent to Drummond Hill (Tirene and Borland's), both of which have been established since 1940 and contain only stands of less than about 6 in. median d.b.h., roe deer have been and are still very numerous, whereas red deer have only been observed during the past 3 or 4 years (Mr J. Kennedy, private communication). Fallow deer have not yet been observed in either area.

Availability of suitable food plants is considered to be important. The decrease of numbers of roe deer since the mid-1940s has occurred even though there was, and still is, a larger area of low-canopy Scots pine on the upper slopes of the forest, which must be structurally similar to those stands at lower levels which were occupied by these animals during former years. But these stands have a field layer which in the main is dominated by heather, and analysis (Table 1) showed few roe deer faeces in such areas.

A number of records by other observers suggests that this pattern of succession of the three species considered here is a fairly general one in Britain. Chard and Stocks (1956), for example, consider that relative abundance of roe deer in the early years following afforestation is a normal event. It is stated (Forestry Commission 1951) that at Thetford Chase Forest 'roe deer had been reintroduced before afforestation began, and have since been present in the young woods in considerable numbers; within recent years red deer, evidently descended from escaped park stocks, have made an occasional appearance'. It was recorded from replies to questionnaires (Taylor 1948) that during the decade 1938-48 roe deer had decreased from 'numerous' to 'not numerous' whereas the numerical status of fallow deer changed from 'not recorded' to 'occasional'. These two records strongly suggest that an earlier period of abundance of roe deer has been followed by their decline and an increase of the numbers of red and fallow deer. Records from Grizedale Forest offer another example. Taylor (1948) records that during the 10-year period 1938-48 numbers of roe deer fell from 'numerous' to 'occasional', red deer were 'numerous' throughout the period, and the rating for fallow deer had improved from 'not recorded' to 'occasional'.

Relative abundance of fallow deer in older forests is illustrated by three examples: First, the fallow deer is the most abundant, though not numerous, deer species in the Forest of Dean 'and very occasionally a stray roe deer has been reported' (Taylor 1956, p. 50); secondly, fallow deer are the most numerous in the New Forest, whereas roe deer and red deer are only locally distributed and less numerous (Forestry Commission 1951); thirdly, there are small herds of fallow deer and 'sometimes a stray roe deer is observed' (Forestry Commission 1950) in the ancient oak and beech woods of the Highmeadow at Tintern Forest.

This pattern of succession explains a number of peculiarities encountered in studies of the distribution of roe deer, some of which are described by Tegner (1951). Tegner noted that roe deer were introduced into Epping Forest, but after many years of moderate abundance, they have now almost all disappeared. Mr E. N. Buxton (quoted by Tegner) considers their disappearance at Epping to be due to the lack of sufficient cover in the forest, a sequence which is completely in accordance with the hypothesis presented in this paper. In similar vein, Mr E. V. Savill is quoted as writing that 'there were a few roe deer left in Windsor Park up to about 10 years ago (1938) but they have now all disappeared. There are, however, still quite a number of roe on this estate near Bagshot'. The Bagshot woods are much younger than most of those in Windsor Park. It is considered to be significant that no other species of deer have been reported in Epping Forest, Windsor Park or Bagshot (Taylor 1948). A consequence of succession such as that outlined is that it makes possible a prediction of the types of forest within which roe, red, or fallow deer 'problems' can be expected to occur. If, for example, it is true that fallow deer tend to become most numerous in mature forest, and that they cause more damage to forest crops than either roe or red deer (Lindemann 1952), then a substantial increase in the numbers of fallow deer and in the damage they cause can be expected as the present extensive areas of young forest in Britain

approach maturity. In general, successive eruptions of each species can be expected if a forest does not contain a complete range of young to old plantations.

The evidence submitted suggests that competition between these species does not have as important an effect upon their distribution in a forest as does the stage of growth of the trees. Delap (1955), Carne (1954, 1955) and Wildash (1951) whose observations were outlined in the introduction, are therefore considered to have misinterpreted their field evidence. It seems more likely that fallow deer have increased in many localities to the 'detriment' of roe deer, not because they are a deterrent (Carne 1954), but simply because the forests have during the same period become older. Thus, also, the co-existence (Delap 1955) of roe and red deer or red deer and fallow deer are considered more likely to be a result of their closer relationships in the sere. Roe deer and fallow deer, supposed to be intolerant of each other (Carne 1954, Delap 1955) are not usually found together in equal abundance because they occupy different kinds of habitat.

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SUMMARY

1. The records of game killed in Drummond Hill Forest and those of other observers indicate that roe deer are usually the most abundant deer in a young forest and that their numbers later decline. Red deer become more numerous at a later stage of development, and fallow deer are most numerous in several older forests.

2. These relationships were also established from the faecal pellet group counts made in Drummond Hill Forest (1957) where it was found that (*a*) roe deer (considered to be a relic population) were uniformly distributed in the stands of different bole sizes on the lower slopes of the forest but were more numerous in two forest blocks adjacent to Drummond Hill which contain only stands of less than 6 in. diameter, and (*b*) red deer were significantly more numerous in forest stands of smaller median diameter than were fallow deer.

3. These and other observations presented are also consistent with the hypothesis that of the several factors which may determine the relative abundance of roe, red or fallow deer, the stage of growth of a forest habitat is more important than inter-specific competition.

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THE BEHAVIOUR OF HONEYBEES VISITING FLOWERS OF FRUIT TREES

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*Rothamsted Experimental Station**

This investigation is concerned with some important aspects of the foraging behaviour of bees on fruit trees about which information was scanty or contradictory.

Bees foraging on fruit trees were chosen at random and continuously observed for as long as possible. Records were made of: whether they collected nectar, or pollen, or both; the way they worked the flowers; the numbers of flowers and trees visited; the length of time they were observed; the reason for observation ending. Table 1 describes the orchards and fruit varieties used. A few observations were also made on other varieties, but the behaviour of bees was similar to that given below.

RESULTS

Bees foraging on apricot, peach, pear, plum, or sweet cherry made the following types of flower visits: (*a*) scrabbled over the anthers to obtain pollen (as described by Parker 1926), and did not attempt to collect nectar; (*b*) stood on the stamens or petals and pushed their tongues and front part of their bodies among the stamens to reach the nectary, invariably touching some of the anthers because of the spreading arrangement of the stamens; (*c*) behaved as in *b* but scrabbled over the anthers for pollen afterwards; or (*d*) behaved as in *b* but scrabbled over the anthers for pollen first. Most bees made either *a* visits only or *b* visits only during observation, but 13·7% of them behaved in two or more of the above ways (Table 2). Nearly all these that behaved in more than one way collected pollen only on some flower visits, and made a mean of 8·3 *a* visits and 7·4 *b*, *c* or *d* visits.

When observation began on a bee the presence or absence of pollen in its corbiculae was noted (Table 3). Except on 6 May (apricots), when pollen was scarce, most bees foraging for pollen only (*a* visits) carried pollen. But bees which were constant to *b* visits often did not, and the proportion of them with pollen varied greatly from day to day; probably such bees were mainly nectar-gatherers but collected pollen incidently when it was obtained readily. Bees making *b* visits packed pollen into their corbiculae only during flight, whereas those making *a* visits often did so on the flowers.

In contrast to the spreading stamens of other species, those of many apple varieties are upright and bees can obtain nectar from them by pushing their tongues between the filaments without touching the anthers or stigma (type *e* visit). Observations were made on five varieties, which differed in the length and

* Work done while on secondment to Ontario Agricultural College.

Table 1. *Orchards in which observations were made*

Species	Location	Date of observation	Mean temperature (° F) during observation	Varieties observed	Mean diameter of trees (ft)	Distance (ft) between adjacent trees	
						In same row	In different row
Peach (*Prunus persica*)	Sandhill's Research Station, N. Carolina	14 March	62·3	Hiland	12·0	15	*
		16 ,,	52·2	,,	,,	,,	
		20 ,,	65·0 (approx.)	Elberta	12·9	,,	20
Apricot (*Prunus armenica*)	Nr. Niagara-on-the lake, Ontario	1 May	52·0	Delicious and Stellas	14·5 (Delicious)	20	20
	,,	3 ,,	55·0	,,	18·9 (Stellas)	,,	,,
	,,	4 ,,	63·9	,,		,,	,,
	Horticultural Exp. Sta., Vineland, Ontario	6 ,,	51·9	Numerous	17·7	25	25
Sweet cherry (*Prunus avium*)	Nr. Queenstown, Ontario	5 May	65·8	Black Tartarian and Early Lyons	16·0	20	25
	,,	7 ,,	65·0	Hedelfingen and Schmidt	22·5	25	25
Plum (*Prunus domestica*)	Nr. Vineland, Ontario	13 May	58·0	Grand Duke and Reine Claude	18·0	20	20
	,,	17 ,,	49·1	,,	,,	,,	,,
Pear (*Pyrus communis*)	Nr. Vineland, Ontario	17 May	51·7	Bartlett and Kieffer	13·9	16	20
	,,	19 ,,	51·6	,,	,,	,,	,,
Apple (*Pyrus malus*)	Horticultural Exp. Station, Vineland, Ontario	22 May	70·6	Red Gravenstein and exp. variety 25051	14·4	18	19
	,,	24 ,,	60·5	Bramley, Oriole and Sandow	14·5	18	19

* Only one row in flower.

thickness of their filaments (Table 4). Experimental variety 25051 and Red Gravenstein were observed on 22 May and the others on 24 May, the variety observed being changed about every 30 min. Varieties with thin filaments (Sandow and 25051) had more *b* than *e* visits but varieties with filaments of

Table 2. *Number of bees which made different types of flower visits during observation (for explanation see text)*

	Peach	Apricot	Sweet cherry	Plum	Pear	Total
a only	148	140	30	54	47	419
b only	122	63	64	56	13	318
c only	2	1	12	0	1	16
d only	1	2	2	0	0	5
a and *b*	29	12	11	4	2	58
a and *c*	3	1	2	0	0	6
a and *d*	1	0	0	0	0	1
b and *c*	3	1	10	1	4	19
c and *d*	0	0	0	0	1	1
a, *b* and *c*	5	5	7	4	5	26
a, *b* and *d*	1	2	0	0	0	3
a, *c* and *d*	1	0	0	0	0	1
b, *c* and *d*	0	0	0	0	2	2
a, *b*, *c* and *d*	2	0	1	0	0	3

medium thickness (Red Gravenstein and Oriole) had more *e* than *b* visits, probably because the greater rigidity and height of the filaments made it more difficult for bees to force their way from the top of the stamens to the nectaries. During many *e* visits to Sandow and 25051 the bees pushed their heads and front part of

Table 3. *Presence of pollen in corbiculae and type of visit*

		Bees constant to *a* visits		Bees constant to *b* visits	
		Pollen present	Pollen absent	Pollen present	Pollen absent
Peach	14 March	69	6	13	21
	16 „	45	7	2	3
	20 „	20	0	63	13
Apricot	4 May	43	1	23	16
	6 „	33	12	2	16
Sweet cherry	5 May	9	1	9	22
	7 „	20	1	19	9
	13 „	14	0	1	1
Plum	17 „	14	0	1	0
	19 „	12	0	1	43
Pear	18 May	27	3	7	5

their bodies among the filaments and often touched the anthers, but during *e* visits to Red Gravenstein and Oriole they could only push their tongues through the more closely spaced and taller filaments and rarely touched the anthers. The thick, closely set filaments of Bramley flowers prevented bees inserting their tongues between them, and although bees probably had more difficulty in making

b visits on this variety than on the two preceding ones, the proportions of *e* visits was lower than with the thin filament varieties. The difficulty bees had in obtaining nectar from the different varieties is reflected in the mean number of flower bees visited per tree: Sandow, 11·5; 25051, 9·7; Red Gravenstein, 8·3; Oriole, 8·4; Bramley, 5·7.

With all species, the percentage of flower visits for pollen only often varied greatly on different days and even at different times on the same day (Table 5). Bees appear to collect pollen only when there is no nectar or it is relatively unattractive; on some days, usually with low temperature, all, or nearly all, visits were for pollen only (16 March, 1, 3, 6, 17 May). On the other days the percentage of visits for pollen only either decreased (4, 5, 18, 19 May) or increased (20 March, 7 May) during observation, or reached peaks at beginning and end of the day (14 March, 13 May).

As the bees were unmarked, there is no proof that the same bees were involved in a general change over from pollen to nectar collection or vice versa during the day. However, this seems likely because some bees visited some flowers for pollen

Table 4. *Behaviour of bees on apple flowers*

Varieties	Length of stamens (mm)		Width of filaments	Number of flower visits of types:					Number bees* which predominantly made visits of types:		
	Mean	Max.		*a*	*b*	*c*	*d*	*e*	*a*	*b*	*c*
Sandow	7·5	8·5	Thin	152	428	22	0	87	3	16	2
Exp. 25051	7·5	9·0	Thin	24	287	12	1	104	1	12	4
Red Gravenstein	10·5	12·0	Medium	27	72	0	0	345	1	2	15
Oriole	12·5	14·0	Medium	85	32	1	3	146	4	1	7
Bramley	13·5	14·5	Thick	98	99	12	1	17	3	5	0

* Visiting 10 or more flowers.

only and others for nectar during the same trip, occasionally changing over from one consistent type of behaviour to another, during observation. Furthermore, on many occasions pollen was still plentiful when most bees were collecting nectar. Exceptions to this condition were in the sweet cherry orchard on 5 May and the plum orchard on 19 May; by the end of observation on these 2 days about half the flowers were denuded of petals, few had any pollen left and nearly all flower visits were for nectar only. In the apricot orchard on 6 May both nectar and pollen were scarce. Bees often approached to within a few millimetres of the flowers without alighting, and appeared able to detect whether or not the flowers had nectar or pollen.

Bees that were constant to one type of visit during observation spent less time per *a* visit than *b* visit for every species except pear (Table 6). No correlation was found between the time of day and duration of visit, possibly because the number of observations were too few to show this.

Observations on a bee ceased either because its identity was no longer certain, it flew off the tree concerned and either disappeared or flew to another tree and

could not be identified, or it went home. A bee going home often first visited one or two flowers on a different part of the tree from that on which it had been working, then cleaned itself (mean duration 27·3 sec: 40 observations) while clinging to a petal or leaf before taking flight, and frequently orientated before finally departing.

Because the bees observed were selected at random, it is likely that, on average,

Table 5. *Percentage of flower visits for pollen only* (*total number of flower visits in parentheses*)

		Hourly periods of observation beginning									
		09·00	10·00	11·00	12·00	13·00	14·00	15·00	16·00	17·00	18·00
Peach	14 Mar.	97 (155)	88 (300)	15 (127)	56 (94)	85 (150)	87 (172)	96 (103)	–	–	–
	16 ,,	–	92 (83)	96 (139)	81 (98)	87 (201)	90 (48)	–	–	–	–
	20 ,,	–	15 (370)	27 (100)	24 (191)	26 (130)	44 (244)	41 (145)	87 (115)	–	–
Apricot	1 May	–	–	–	100 (243)	100 (120)	–	–	–	–	–
	3 ,,	–	–	100 (178)	100 (82)	–	–	–	–	–	–
	4 ,,	–	85 (254)	53 (86)	82 (226)	70 (183)	56 (323)	44 (267)	54 (377)	0 (3)	–
	6 ,,	–	88 (428)	85 (313)	73 (291)	87 (337)	78 (488)	–	–	–	–
Sweet cherry	5 May	–	28 (76)	48 (474)	14 (147)	5 (411)	5 (259)	1 (486)	–	–	–
	7 ,,	–	–	24 (107)	46 (110)	34 (250)	57 (317)	65 (221)	–	–	–
Plum	13 May	–	100 (70)	83 (160)	–	–	–	42 (24)	56 (45)	84 (219)	–
	17 ,,	–	98 (203)	99 (76)	100 (14)	100 (4)	–	–	–	–	
	19 ,,	–	–	–	100 (22)	–	89 (343)	69 (261)	44 (161)	24 (152)	0 (112)
Pear	17 May	–	–	–	–	–	–	100 (83)	100 (59)	–	–
	18 ,,	100 (38)	44 (139)	90 (118)	46 (171)	42 (45)	8 (206)	19 (220)	3 (108)	27 (127)	–

they were near the middle of their visit to the tree concerned and altogether visited twice as many flowers before leaving it as they were seen to visit. The number of flowers bees visited per tree was estimated on this basis (Table 7). Information on bees whose identity became uncertain before they left a tree is not included in the calculation. Similarly, doubling the mean number of flowers seen to be visited, on one or more trees, by bees which were followed until they flew home gives an estimate of the mean number of flowers bees visited during a

complete trip. Using this information to calculate the number of trees visited per trip (Table 7) gives, if anything, an under-estimate because, owing to the difficulty of following a bee for numerous flower visits and especially from tree to tree, the bees which were observed until they flew home probably tended to be nearer the end rather than the beginning of their trips.

Two pollen-gatherers and two nectar-gatherers were observed for what were most probably complete trips; the pollen-gatherers made 89 (apricot) and 38 (pear) *a* visits respectively and the nectar-gatherers made 76 (pear) and 82 (sweet cherry) *b* visits.

Observations on peach flowers did not record when bees returned home, and so the number of trees visited per trip could not be calculated. However, the peach

Table 6. *Mean time (sec) per flower visit (number of flowers in parentheses)*

	Peach			Apricot	
	a visits	*b* visits		*a* visits	*b* visits
14 March	14·4 (681)	32·3 (166)	1 May	10·9 (358)	–
16 ,,	15·9 (350)	24·4 (12)	3 ,,	8·8 (197)	–
20 ,,	15·7 (251)	19·9 (671)	4 ,,	7·3 (1018)	12·2 (395)
			6 ,,	6·8 (1447)	9·0 (292)
Total	15·0 (1288)	22·4 (849)	Total	7·6 (3020)	10·8 (687)

	Sweet cherry			Pear	
	a visits	*b* visits		*a* visits	*b* visits
5 May	9·3 (268)	9·5 (789)	17 May	10·0 (109)	–
7 ,,	8·7 (270)	11·0 (436)	18 ,,	9·1 (320)	7·8 (435)
Total	9·0 (538)	10·0 (1225)	Total	9·3 (429)	8·8 (435)

	Plum			Apple		
	a visits	*b* visits		*a* visits	*b* visits	*e* visits
13 May	5·8 (380)	16·5 (74)	22 May	6·2 (4)	8·9 (107)	11·9 (104)
17 ,,	7·3 (247)	–	24 ,,	5·5 (221)	7·5 (273)	10·4 (91)
19 ,,	4·8 (523)	16·0 (351)				
Total	5·6 (1150)	15·6 (436)	Total	5·5 (235)	7·9 (380)	11·2 (195)

trees were small with few flowers so it was not so difficult as with other species to follow bees from tree to tree. Bees foraging on peach flowers evidently behaved very differently from those on other species, because the mean number of trees visited during observation and the mean number of flowers visited per tree was 2·3 and 4·2 respectively for 147 bees which made *a* visits only, and 2·3 and 3·2 for 123 bees which made *b* visits only. The numbers of trees visited increased with the numbers of flowers visited (Table 8). Even if the mean number of flowers visited was as low as half the maximum observed, the bees would have visited as many as four or five trees a trip.

The mean number of flowers visited per tree varied from day to day (Table 9). In general, with the same varieties, on relatively favourable days when there were

Table 7. *Number of flowers visited per tree and number of trees visited per trip*

	Mean number of flowers (x) visited per tree during observation (number of trees in parentheses)	Probable mean number of flowers visited per tree ($2x$)	Mean number of flowers (y) visited by bees which probably returned home at finish of observation (number of bees in parentheses)	Estimated mean number of flowers visited per trip ($2y$)	Estimated mean number of trees visited per trip (y/x)
Apricot (Niagara-on-the-lake)					
Type *a* visits	16·8 (78)	33·6	25·8 (9)	51·6	1·5
Type *b* visits	8·4 (56)	16·8	17·7 (3)	35·4	2·1
Apricot (Vineland)					
Type *a* visits	26·8 (40)	53·6	46·3 (13)	92·6	1·7
Type *b* visits	12·6 (19)	25·2	13·6 (7)	27·2	1·1
Sweet cherry					
Type *a* visits	17·5 (26)	35·0	26·9 (8)	53·8	1·5
Type *b* visits	13·7 (88)	27·4	37·4 (12)	74·8	2·7
Plum					
Type *a* visits	17·4 (56)	34·8	28·3 (14)	56·6	1·6
Type *b* visits	5·4 (71)	10·8	7·3 (14)	14·6	1·3
Pear					
Type *a* visits	9·2 (56)	18·5	15·3 (17)	30·6	1·6
Type *b* visits	21·7 (16)	43·4	43·8 (6)	87·6	2·0
Apple					
All types of visit	9·8 (85)	19·6	22·1 (11)	44·2	2·2

a considerable number of *b* visits (*i.e.* peaches, 14 March; apricots, 4 May; plums, 19 May; pears, 18 May; see Table 1) the bees visited more flowers per tree and spent less time per flower than on less favourable days. Records were too few to establish any relationship between the time of day and the number of flowers visited per tree, especially because some bees were obviously satisfied with the crop when others were not. But, in unfavourable weather, and particularly just

Table 8. *Number peach flowers and trees visited per observation*

	Type *a* visits		Type *b* visits	
Number of flowers visited	Number of bees observed	Mean number of trees visited	Number of bees observed	Mean number of trees visited
1- 5	69	1·2	70	1·3
6-10	29	2·0	25	2·9
11-15	19	3·3	14	3·6
16-20	11	3·4	7	5·0
21-25	9	4·3	3	5·0
26-30	6	4·8	0	–
31-35	0	–	2	5·0
36-40	0	–	0	–
41-45	2	7·0	1	7·0
46-50	1	7·0	0	–
51-55	1	8·0	1	7·0

before rain, bees frequently flew from tree to tree, often without even alighting on the flowers. However, on favourable days when many bees were foraging, they appeared to disturb each other more, so that many of them took flight, sometimes going to another tree. In some orchards the distance between rows of trees was

Table 9. *Mean number of flowers visited per tree on different days (number of trees in parentheses)*

	Peach			Apricot	
	a visits	*b* visits		*a* visits	*b* visits
14 March	4·6 (170)	2·8 (66)	1 May	12·1 (30)	–
16 ,,	4·1 (99)	1·8 (12)	3 ,,	13·7 (19)	–
20 ,,	3·5 (73)	3·4 (209)	4 ,,	17·8 (59)	8·4 (56)
			6 ,,	26·8 (40)	12·6 (19)

	Sweet cherry			Pear	
	a visits	*b* visits		*a* visits	*b* visits
5 May	28·7 (6)	17·9 (44)	17 May	6·8 (21)	–
7 ,,	14·5 (19)	8·2 (38)	18 ,,	10·7 (35)	21·7 (16)

	Plum			Apple
	a visits	*b* visits		All types of visit
13 May	16·1 (20)	6·1 (73)	22 May	9·0 (42)
17 ,,	9·5 (19)	1·0 (1)	24 ,,	7·4 (28)
19 ,,	26·6 (16)	5·4 (58)		

greater than between trees in the same row, and bees flew more frequently between trees in the same row than between trees in different rows (Table 10).

Sweet cherry trees had more bees on their sunny sides than on their shady sides, although the latter were more protected from a strong wind prevailing at the time

Table 10. *Effect of greater distance between rows than between trees in a row*

	Distance between trees (ft)		Mean diameter of trees (ft)	Mean distance (ft) between edges of trees in:		Number of bees changed to trees in:	
	Same row	Adjacent row		Same row	Adjacent row	Same row	Adjacent row
Pear	16	20	13·9	2·1	6·1	34	5
Peach	15	20	12·9	2·1	7·1	146	72
Sweet cherry	18	25	16·0	2·0	7·0	27	11

(Table 11). This difference was also found with Stellas apricot trees but not with Delicious apricot trees which were every third tree in the same rows as the Stellas. The Delicious trees were smaller than the Stellas (mean diameter of 14·5 and 18·9 ft respectively), much less dense and with fewer flowers, and more light passed through them.

DISCUSSION AND CONCLUSIONS

Parker (1926) observed that bees visiting apple, cherry, plum or pear flowers collected either nectar only, pollen only, or both. However Vansell (1942) working with cherry and peach, and Stephen (1958) with pear, found that nectar-gatherers became covered with pollen, and Brown (1951) found that bees visiting plum flowers collected either nectar or pollen, but never both during the same trip. My results agree with those of Parker (1926), and although all bees collecting nectar from every species except apple touched the anthers, only about half collected pollen as well, probably doing so incidently when the pollen was readily available. A few bees deliberately collected pollen as well as nectar on the same visit, scrabbling over the anthers in the same way as bees collecting pollen only.

The upright stamens of apple flowers allow bees to obtain nectar without touching the anthers (Brittain 1933, Free 1958). My results show that the proportion of nectar-gatherers which do so depends on the structure of the stamens, and if the stamens are flexible enough, bees prefer to approach the nectary from the top of the stamens, as in the other species studied. Preston (1949) believed that

Table 11. *Mean number of bees on sunny and shady side of trees (number of trees in parentheses)*

			Sunny sides	Shady sides
Apricots	Row 1	Delicious	0·6 (15)	0·5 (15)
		Stellas	7·9 (9)	2·9 (9)
	Row 2	Delicious	0·8 (15)	0·9 (15)
		Stellas	10·8 (10)	5·1 (10)
	Row 3	Delicious	1·8 (19)	1·6 (19)
		Stellas	17·9 (10)	8·1 (10)
Sweet cherry	Row 1		1·6 (20)	1·0 (20)
	Row 2		2·9 (20)	0·6 (20)

the tall, thick stamens of Bramley apple flowers prevented honeybees from reaching the nectaries; this has been confirmed. Probably the behaviour differences observed on different apple varieties are more consistent in orchards with only one or two varieties present, than in the experimental orchard which contained numerous varieties.

Although individual bees tended to be constant to one type of flower visit during a single trip, certain bees visited some flowers for pollen only and others for nectar during the time they were observed. It is unlikely that these bees were primarily pollen-gatherers which were taking only enough nectar to sustain themselves, because they made similar numbers of flower visits for pollen only and for nectar.

The ratio of nectar-gatherers to pollen-gatherers, and probably the behaviour of individuals, varied greatly on different days and at different times on the same day, and bees apparently can often collect pollen when nectar is either unavailable or unattractive. These results agree with those of Brittain (1933) on apple.

A bee does not forage at random over a crop but tends to restrict itself to a

small part of it (Minderhoud 1931, Buzzard 1936, Butler, Jeffree & Kalmus 1943), and Minderhoud (1931) supposed that large fruit trees, well separated from others, might not be sufficiently cross-pollinated. MacDaniels (1931) said that a bee tends to keep to one tree, or two adjacent trees, and Singh (1950) found that 45 out of 66 bees kept to one apple tree during observation. Because of the difficulty in maintaining continuous observation on a bee, and especially in following it from tree to tree, I could not obtain definite information on the number of trees a bee visits during a single trip, but relevant calculations indicate that, on the average, bees probably visit two or more.

During relatively unfavourable conditions, bees tended to spend more time per flower and visited fewer per tree than in favourable conditions. The observed extension of foraging areas in unfavourable circumstances agrees with observations on the behaviour of bees on artificial food sources (Butler *et al.* 1943) and indicates that, although fewer bees may be foraging in such circumstances, they are individually more valuable as cross-pollinators. Bees collecting nectar change trees more frequently than those collecting pollen only, but as they also spend more time per flower visit, and are probably less efficient pollinators, particularly of apple, they are probably less valuable as cross-pollinators.

SUMMARY

1. Foraging bees were watched on apple, apricot, peach, pear, plum and sweet cherry flowers.

2. During a single flower visit a bee either approached the nectary from the top of the stamens, sometimes collecting pollen in the process, or scrabbled over the anthers and gathered pollen only, or, far less often, did both. Bees also obtained nectar from apple flowers by inserting their tongues between the filaments of the stamens from the side, often without touching the anthers; the proportion of nectar-gatherers that visited the flowers in this way varied with the flexibility, height and thickness of the filaments of the variety concerned.

3. During a single trip or part of a trip most bees kept to one type of behaviour, but some collected pollen only on some flower visits, and nectar, with or without pollen, on others.

4. The proportions of the different types of flower visits varied from day to day and at different times on the same day. Pollen was sometimes collected when little or no nectar was collected, and on two occasions when the flowers concerned were nearly denuded of pollen, the majority of bees collected nectar only.

5. Except on pears, pollen-gatherers spent less time per flower and visited more flowers per tree than nectar-gatherers. On unfavourable days bees spent longer per flower and visited fewer flowers per tree.

6. Bees probably visited two or more trees per trip and tended to change to trees nearest to those on which they started working.

7. More bees foraged on the sunny than on the shady sides of trees.

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A NOTE ON THE DISTRIBUTION OF THE COYPU (*MYOCASTOR COYPUS*) IN GREAT BRITAIN

By R. A. DAVIS and A. G. JENSON

Ministry of Agriculture, Fisheries and Food

(With 1 Figure in the Text)

DISTRIBUTION IN 1946

Laurie (1946) gave an account of the occurrence of the coypu (*Myocastor coypus* Molina) in Great Britain. At that time, thriving wild colonies had become established in parts of East Norfolk, and on a sewage farm near Slough in Buckinghamshire. These colonies originated from escaped coypus from fur farms, most of which were in the southern and south-eastern counties of England. The fur farms were given up in 1939 because of the war, but escapes had occurred before then, from as many as half of the farms that were known to have existed. By 1945 the species was well-established in parts of East Norfolk.

DISTRIBUTION SINCE 1946

From 1954 to 1956, short surveys showed that the animal had extended its range well beyond that noted by Laurie. Individual coypus have been seen on the coast from time to time, even in the littoral zone. This is not altogether surprising, since the animal is sometimes estuarine in S. America and eats molluscs as well as aquatic vegetation; in Britain, it eats the fresh water mussel, *Anodonta cygnea*.

The map (Fig. 1) shows the known qualitative distribution in 1944, and the situation as known to staff of the Ministry of Agriculture in February 1959. Quantitative information on occurrence is not easy to obtain, since the animals appear to move about the countryside seasonally to some extent, according to the weather and the crops being grown. Furthermore, in cold wintry weather, more animals are seen in the daytime than usual, since the coypu is normally crepuscular to a large extent. Consequently, populations have to be assessed largely by trapping, and by the presence of recently used runs, fresh droppings and grazed vegetation or damaged crops. Trapping, marking and releasing work is being carried out, and will be separately reported in due course.

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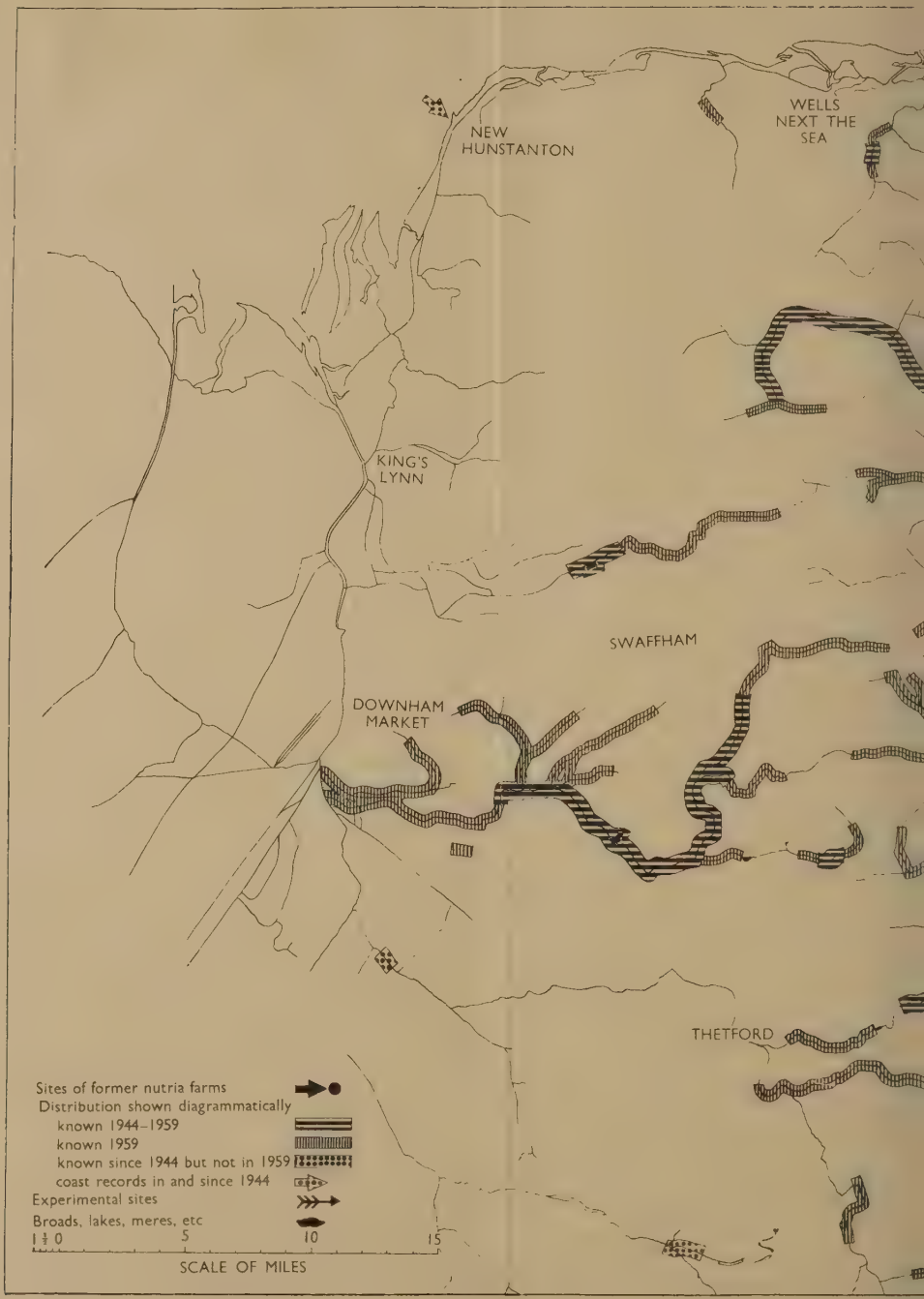
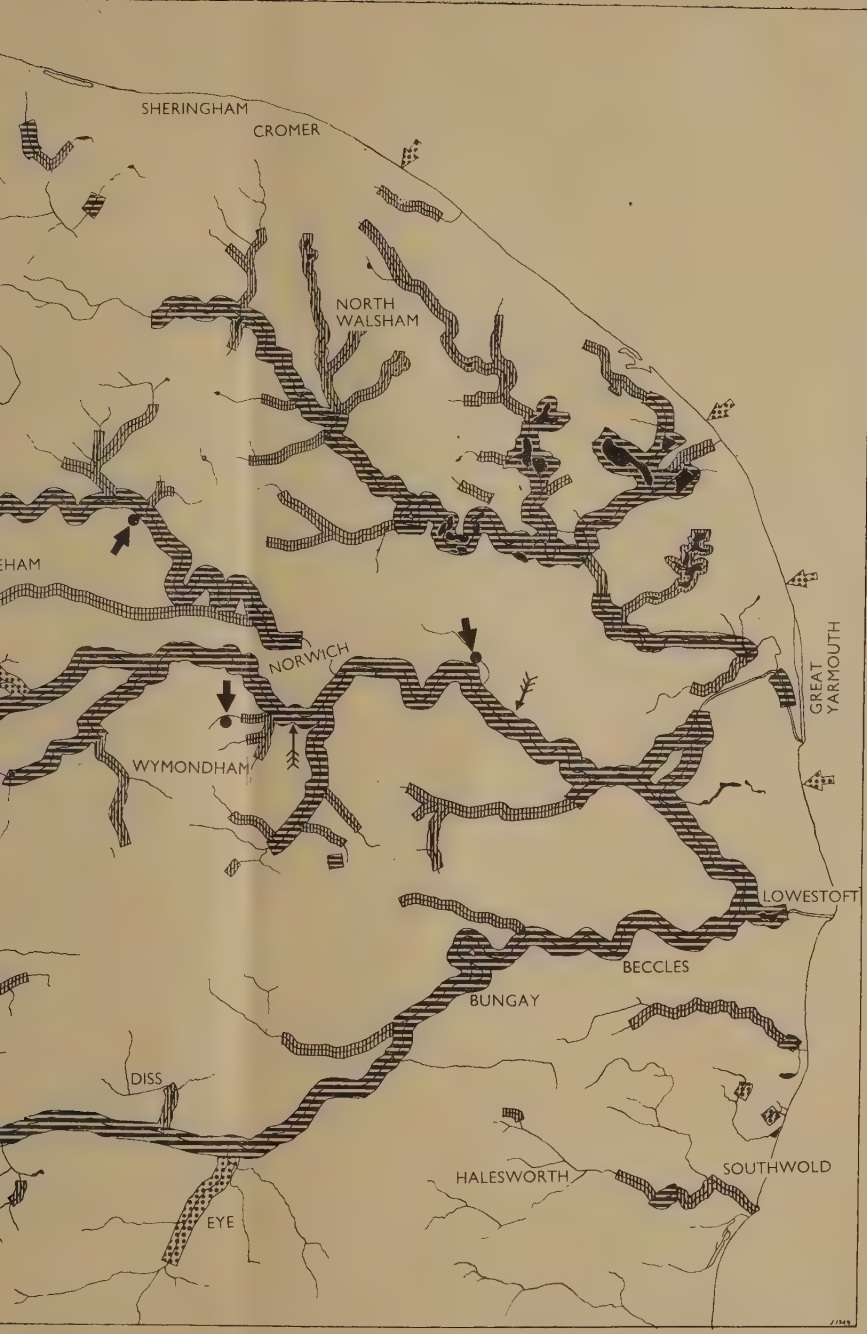


Fig. 1. The distribution



pu in Britain.

KEY FACTORS IN POPULATION STUDIES

By G. C. VARLEY and G. R. GRADWELL

Hope Department of Entomology, Oxford

(With 1 Figure in the Text)

Morris (1959) has introduced the term *key-factor* for mortality factors which 'cause a variable ... mortality and appear to be largely responsible for the observed changes in population' density in successive generations. In his paper Morris illustrates a statistical method designed to determine whether or not mortality at one stage is, at least in part, caused by a key factor. Here we give a simple alternative method of identifying the stage at which a key factor is operating using an extention of Haldane's (1949) logarithmic method for comparing the different killing powers of a series of successive mortality factors acting on a population. Haldane wrote an equation for the total mortality $K = k_1 + k_2 + k_3 \ldots$ where the k-value for each mortality is the difference between logarithms of numbers per unit area before and after its action. In his example he used Napierian logarithms but we prefer to use common logarithms.

Our method is to calculate the k-values for each estimated mortality over a number of years and plot them against time. The contribution of each mortality to the variation in K can be seen by inspection, or can be studied statistically. Mortality caused wholly or in part by a key factor is recognized since its k-values will change with time in the same way as the changes in the total mortality. If this method is applied to cases like those considered by Morris where the only available information is a series of annual counts of population and the percentage parasitism it will reveal whether the parasites are the key factor or not.

In our study of the population dynamics of the winter moth (*Operophtera brumata* (L.)) at Wytham, Berkshire, we have estimated the numbers at two stages of the life cycle each year, and can calculate the k-values between each estimate. The k-value of the mortality caused by some parasites has been separately assessed, but often many factors contribute to the measured mortality over a certain period. Fig. 1 shows plots of these k-values, and we see immediately that the shape of the curve of k_1 is very like that of K, hence the mortality which we call winter disappearance includes that which is due to the key factor. Winter disappearance includes all the mortality from the time the adult moths are sampled in November and December to the subsequent count of fully fed larvae in May, and is calculated on the basis of an assumed constant egg production. It thus includes variations in female mortality and in egg production as well as mortality in the eggs and newly hatched larvae. In a previous paper (Varley & Gradwell 1958) we found that winter moth suffers 'the greatest proportionate loss in the first larval stage. Survival at this stage is very variable from year to year, probably owing to weather factors. These differences go far to explain the big

changes in population density, which are often synchronous over a wide area.' This new method of presenting the observations, now extended for a further 4 years, serves to confirm this earlier conclusion.

The graphs show also that the change in k_1 the winter disappearance is usually greater than the change in K, and that pupal predation k_5 is partly compensating for changes in winter disappearance. This effect has already been reported (Varley

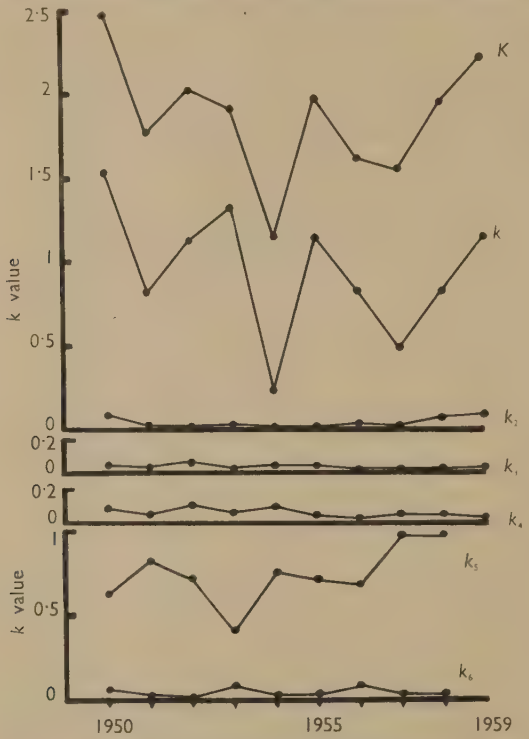


Fig. 1. Mortality affecting winter moth 1950-9 at Wytham, Berkshire, on logarithmic scale.
K, total mortality $= k_1 + k_2 \ldots k_6$;
k_1, winter disappearance;
k_2, Tachinid parasite of larva, *Cyzenis albicans* (Fall.);
k_3, other larval parasites;
k_4, disease (Microsporidian);
k_5, pupal predators;
k_6, pupal parasite, *Cratichneumon culex* (Müll.).

& Gradwell 1958, Table 1) since pupal predation in any one year was higher under trees with a high pupal population than under adjacent trees with low populations. The graphs of the k-values provide a simple alternative method of revealing it.

A further discussion of the nature and role of the mortality factors in the population dynamics of winter moth will be published at a later date, but we hope that this illustration of our method for identifying the cause of population change will be of immediate use to other workers.

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REVIEWS

THE EUROPEAN COLLEMBOLA

Hermann Gisin (1960). *Collembolenfauna Europas.* Pp. 312; 554 text-figures. Geneva: Musée d'Histoire Naturelle. Price Swiss Fr. 24.00.

It is only in recent years that ecologists have come to realize that the Collembola occur in tens of thousands in every square metre of most soils and in a great range of habitats, from arctic tundra to hot houses, from caves to the roofs of buildings. The estimation of their ecological significance has been greatly hampered by the lack of an up-to-date and comprehensive taxonomic work, and it is precisely this need which is met by the volume under review. Dr Gisin, who has himself made important contributions to the ecology of the group, has set out with this object in view.

The layout of the work, with running headings to the pages and a complete index, is most convenient and it covers all Collembola described from Greenland to the Urals and the Mediterranean up to the beginning of 1959. Again, Dr Gisin's abhorrence of splitting, name changing and the multiplication of new genera (he has been responsible for the official 'sinking' of many of these) results in a new work which can be adopted with a minimum of trouble; the Collembola are still divided into five familiar families and fifty-four well known genera. Where genera have become unwieldy the optional use of subgenera is suggested, but only one new subgeneric name is introduced in this work. This does not mean that the book is merely an enlargement of Gisin's *Hilfstabellen* of 1943.

There is now a total list of some 850 species, about 200 of which are recognized as British. The keys contain many new criteria for distinguishing species, and these are illustrated by clear line diagrams. There are separate groups of keys to families, to genera and then to species and the keys to genera are illustrated by outline drawings which will be invaluable to the beginner. Under each species appears a full diagnosis followed by notes on distribution and habitat, bibliography and points on aberrant forms. The introductory section begins with morphological notes, conventional formulae, the determination of sex and stage of development, mounting techniques, and the conditions which should be observed before the novice in his enthusiasm inflicts on the literature yet another doubtful new species. The taxonomy of the Collembola, particularly in Britain, has indeed been bedevilled by unreliable descriptions, and the impulse of a less careful author might have been to make a drastic revision of the group. Gisin has included many doubtful species with suitable warning, but the discrepancy between Kloet & Hinks's figure of 261 species and Gisin's of less than 200 indicates the number of very doubtful species which he has omitted. Certain genera, especially *Onychiurus*, which now contains 134 species, have been greatly expanded by recent work, and some of the additions may lead to controversy. Gisin has produced evidence that very trivial morphological differences may correspond with marked ecological specializations, and it seems clear that many species should be recognized in these ubiquitous genera. Presumably only breeding experiments will finally settle some of the disputed cases.

In the production of this volume, Dr Gisin has added yet another service to soil ecology; there can be no doubt that it will enjoy a long and useful history and that it deserves translation into the English language; it is the more satisfactory to find that the price is most reasonable.

A. MACFADYEN

BIOLOGY OF DRAGONFLIES

Philip S. Corbet, Cynthia Longfield & N. W. Moore (1960). *Dragonflies.* Pp. xii+260, 53 coloured illustrations; 16 photographs; 200 text-figures. London: Collins (New Naturalist, No. 41). Price 42*s*.

Books on British dragonflies reflect the changing trend of fashion in biological thinking. In 1900, as the great age of systematics was nearing its close, Lucas published a handbook which enabled workers to name their captures. In 1917 appeared Tillyard's well-known book *The Biology of Dragonflies*, most of which was devoted to morphology and evolution, an attitude to zoology which was just beginning to give way to that of a generation who wanted to know how animals worked. The next book (1937) should, therefore, if my opening statement were quite correct, have been on the physiology of the group, but in fact it was another handbook, this time by C. Longfield. The work under review, not intended to replace but rather to be set beside the earlier ones, is right in the van of current fashion and perhaps more than any other in the series merits the words 'new' and 'naturalist'. Taxonomy, morphology and physiology are mainly indoor occupations, and for almost a century many zoologists have found little need to know much about the living animal in its natural setting, to which study, however, their findings must ultimately lead. Dr Corbet and Dr Moore are keen exponents of the practice of watching natural phenomena, no matter how inconvenient the time of day or how inclement the time of year at which they take place. The life history of the dragonfly has been known for centuries, but until recently nobody could say precisely how long the eggs of any one species took to complete development, how long the nymphal life lasted and when growth took place, where and under what conditions emergence happened, how many adults, soft and helpless just after the process, were taken by predators, or just how the adults spent their time once they could fly. These are the questions which, for some of the species, Corbet and Moore have set out to answer, and they have brought to their field observations a sound background of conventional teaching. Corbet inclines to the Cambridge school and has studied the incidence of diapause in the life history of various species, whereas Moore, interested in adult behaviour, acknowledges a debt to Tinbergen and Lorenz. It is pleasing to see these two collaborating with Miss Longfield who has done so much to bring together the scattered random observations which collectors amass. These, scorned as 'unscientific' by some professionals, for whom 'Natural History' has a pejorative meaning, provide a foundation and formulate the problems for those who, by means of regular and painstaking observations take knowledge a step further.

The book starts with some general facts for those with little knowledge of entomology, and with some general remarks about the British species. From chapter 3, misleadingly entitled 'History of the British Dragonflies', readers may learn something of the people who have hitherto been to many of them no more than the authors of the various species. The maps showing world distribution in the next chapter will be found very useful, though, as always, the reader hankers to know which white areas denote absence of dragonflies and which absence of entomologists. The text, however, shows a certain lack of acquaintance with recent ideas and there is no mention of Thienemann's authoritative 800-page work on the history of the European freshwater fauna. There follow seven chapters which include much of the modern work of Corbet and Moore already mentioned. Chapter 12 on fossil history seems out of place in a book by keen observers of the living animal, though this may be personal bias. Chapters on dragonflies and other animals and dragonflies and man are useful but caudal.

Appendix 1, a reprint of Mr A. E. Gardner's key to the larvae, will be welcomed though, a small point, it is a pity that the opportunity has not been taken to rid it of

some of its archaic phraseology; the beginner must still decide whether a lamella is nodate, subnodate or denodate and can find out what those words mean only by comparing the illustrations. To point out that the separation of one or two species is still not entirely satisfactory is not to disparage the excellent work which Mr Gardner has done on the group.

All three authors indulge in speculation and do not always reach the same conclusions. The reader will enjoy deciding for himself which he finds most convincing, but I would like to utter a warning against the suggestion that the life history of rare and scarce species can be discovered by pooling information gained from various places over the years, because some unpublished results of mine indicate a different life history in different parts of one pond, probably on account of the amount of food available. None of the authors is specially interested in population dynamics, but they do provide data about several species for anyone who is. It remains to discover more about the number of eggs laid and about the mortality of nymphs in the early stages. Ecologists may also like to learn that surprisingly little is known about the factors limiting the range of any species. The authors quote what they refer to as the pioneer work of Steiner on choice of an oviposition site, but do not mention the ferocious attack launched on it by Schiemenz. Corbet has an ingenious theory which correlates the various life histories with different degrees of adaptation of a tropical group to a temperate climate. Moore stresses the importance of competition between adults, but I think that both would agree that the main value of their hypotheses lies in the indication they give of the direction which further observations and experiments should take.

There are 53 illustrations in colour by Mr S. Beaufoy whose success in photographing insects is well known to those familiar with the New Naturalist series. Among the black and white photographs Corbet's studies of *Anax imperator* mating and laying eggs are noteworthy.

T. T. MACAN

MARINE PHYSIOLOGY

J. A. Colin Nicol (1960). *The Biology of Marine Animals.* Pp. xi + 707; 294 text-figures. London: Pitman. Price 95*s*.

This large book is an impressive production, though its price may well put it beyond the reach of most students. The word 'biology' in the title is a little misleading, for there are not many references to marine ecology in the book. One example is on p. 75 in the section on water, salts and minerals, where the author briefly mentions the importance of osmotic control by an estuarine polychaete. In this case the egg, which is itself without the power of osmotic control, is surrounded by a thick coat of jelly in which it can develop even in distilled water; the larva, when it hatches, becomes able to control its osmosis and so can colonize such difficult environments as estuaries. This polychaete is contrasted with a mussel of the open coast whose eggs and larvae are alike unable to cope with osmotic changes and so cannot tolerate the mildest of estuarine conditions. One would have welcomed many more illustrations of this apt and illuminating kind; perhaps the book's title should have been 'Life Processes' or 'The Physiology' of marine animals.

As a physiological account this book is very well organized. It is divided into no more than 15 chapters, each of which has excellent and helpful headings and sub-headings and is followed by a list of some 50 to 100 or more references to the literature. It is sometimes annoying when an author divides up his references in this way, but in this case the practice is abundantly justified, for each chapter can stand by itself as a full account of its particular subject. The field covered is a wide one, extending as it does

from osmotic relationships through respiration, feeding, the nervous system and colour to associations with other animals and plants and skeletal modifications, etc. There is also, as one would expect from Dr Nicol, a particularly authoritative chapter on the production of light by marine animals. The author tells us that the book took 6 years to prepare; this one can well believe, for the literature which has been culled is immense. The book has also taken a long time to produce; the author's preface is dated 1956, and there are, in consequence, few references to work published in 1957, and hardly any for 1958.

In spite of what has been said above, however, it is difficult to be wholly enthusiastic about this book, for it does contain some blemishes. There is a large index, but this is not complete; in Chapter 2, for example, the figures have been indexed, but it seems that both text and tables have been omitted. There are one or two slips, some of them rather misleading, in the figures; for example, in Fig. 2.19 on p. 75 salinity curves are marked as percentages of concentration (or dilution?) of sea water; on p. 98 Fig. 3.4 reads from right to left, and Fig. 3.5 (immediately below) reads from left to right, but this is not made clear in the legend; in Fig. 12.2 (p. 542) the words *left* and *right* should be transposed. The most serious fault of the book, however, is its style, which betrays the author's love of jargon-words and makes the book in places unnecessarily difficult to read; for example, 'treatment by curare' is surely preferable to the rather dreadful word 'curarization' (p. 400). Sometimes this use of jargon affects whole sentences, as in the following one on p. 462: 'olfaction is the dominant sensory modality in some species; tactile or visual sensations in others'; this could have been written as—'smell is the most important sense in some species, touch or sight in others'—without, as far as I can see, losing any of its meaning.

Having made the above strictures (or carpings?) I must stress once more that *The Biology of Marine Animals* is in general a thorough and valuable book, packed with interesting information; it is an essential item on the shelves of any marine biological library.

JOHN S. COLMAN

ECOLOGY AND POLLUTION

H. B. N. Hynes (1960). *The Biology of Polluted Waters.* Pp. xiv+202; 2 plates; 22 text-figures. Liverpool: University Press. Price 25*s*.

Dr Hynes, in the writing of this book, has tackled a difficult subject extremely well. Although an invertebrate ecologist of distinction, he has been actively engaged in general studies of pollution for several years and this book achieves a balance which reflects the wide interests and extensive experience of the author.

The introductory chapters describe the history of pollution mainly in Great Britain, systems of classification of lakes and rivers, and ecological factors which are of importance in determining the distribution of plants and animals. The second part of the book deals with the biological effects of pollution. The author discusses the effects of poisons, suspended solids, organic matter and hot water on biological communities. The penultimate chapter contains a critical appraisal of biological investigations and a discussion of the dangers of rigid classification systems developed to assess the severity of pollution by referring to groups of indicator species. Dr Hynes ends his book with a glance into the future, reviewing what now appear as rather unconventional methods of effluent treatment and utilization.

Certain themes emerge quite clearly which are of such importance that anyone involved in the administration of water-courses should read this work. The most pertinent is the reluctance of authorities to carry out biological investigations and their

reliance on chemical analyses. The author stresses the limitations of both chemical and biological approaches and the need for collaborative studies. Another timely reminder concerns the very limited value of fish toxicity tests which are not closely linked with observational data.

The reviewer disagrees with only one statement in the text (p. 22) that 'aquatic angiosperms apparently absorb their nutrient salts from their roots and not directly from the water'. Several aquatic angiosperms have rudimentary rooting systems and there is a body of physiological evidence which suggests that plants are able to absorb nutrients through leaves and stems. There are certain ambiguities in the description of the activated-sludge process (p. 56). The illustrations are generally of a high standard and there is an extensive bibliography.

This book should be of interest and value not only to the freshwater biologist but also to all those who are associated with pollutional problems.

R. W. EDWARDS

AMERICAN HERONS

Andrew J. Meyerriecks (1960). *Comparative Breeding Behaviour of Four Species of North American Herons.* Pp. viii+158; 15 plates; 39 text-figures. Cambridge, Mass.: Nuttall Ornithological Club (Publ. No. 2). Price $2.00 (paper) or $3.00 (cloth).

An understanding of the ecology of any species requires a detailed knowledge of its life history and behaviour. Until recently, however, scientific periodicals have provided few opportunities for the publication of detailed life history studies. The inauguration of a monograph series by the Nuttall Ornithological Club is thus of considerable importance. This, the second in the series, contains a detailed study of the green heron (*Butorides viriscens*) and considerable additional data on *Ardea herodias*, *Dichromanassa rufescens* and *Leucophoyx thula*. The observations were made in the eastern United States, where the author spent several thousand hours in the field. In each case details are given of migration, feeding behaviour, pair formation, hostile and aggressive displays and many other aspects of breeding biology. The material is primarily descriptive, but the comparative approach throws considerable light on evolutionary trends within the group. In a final chapter the author discusses a number of general topics, such as the evolution of social nesting within the group, and the significance of polymorphism. He suggests that the white coloration, which occurs in many members of the group, is related to conspicuousness in a social situation, and that the changes in the coloration of the soft parts have a display function. Of particular interest are the differences between species in the variety of feeding methods employed. In general, the feeding behaviour of the larger species is inactive, involving the 'stand and wait' or 'wade slowly' techniques. By contrast, the smaller species use a variety of methods, often involving 'disturb and chase' techniques. The green heron is an exception to this rule: the author regards this as indicative of relationship to the bitterns.

R. A. HINDE

SCHOOL ECOLOGY

W. H. Dowdeswell (1959). *Practical Animal Ecology.* Pp. 316; 16 plates; 86 text-figures. London: Methuen. Price 32*s.* 6*d.*

There is little doubt, as the author of this book points out, that ecology is one of the most difficult branches of biology both to teach and to learn; and at an elementary level

the study of an animal community presents far greater problems than does one of plants. In addition the last ten years have seen a big increase in ecological research, with development of new apparatus and new methods of approach. For these reasons a really practical book, such as the present work, will be widely welcomed by teachers and more senior students.

Books of this nature are sometimes full of learned accounts of apparatus and techniques for measuring everything that might affect an organism, but with little or no mention of the living organism itself. This can be most depressing to the teacher-naturalist who may not be clever at making apparatus, or who may not have a technician to make it nor money to buy what he wants. It can even misdirect teachers by giving them the impression that there is nothing more to ecology than measuring and using a few techniques. This I saw very clearly some years ago when a certain university department came to a field centre with so much expensive textbook equipment that the sites where the students worked had to be chosen for accessibility to vehicles; and at the end of the week those students were wondering what on earth it was all about. The living organisms had been forgotten in the enthusiasm of measuring factors and using techniques. I was glad to find that Mr Dowdeswell's book did not depress me in this way. In fact it is thoroughly 'down to earth' and full of valuable information which it would be impossible to find gathered together in any other volume.

There is first a chapter describing modern methods of measuring the more important climatic factors: temperature, light, humidity, current, gases dissolved in water, pH, and dissolved minerals. Collecting and marking methods are discussed next, with useful footnotes giving addresses of firms or references to original papers. Two chapters on quantitative ecology are valuable and provide a simple account of sampling and the use of statistical methods in analysing ecological data. By means of actual examples, the most non-mathematical biologist can in fact learn something of statistics as a tool, without the pain of trying to understand the formulae. The author points out in his preface that the ecology of soil is a subject which is admirably suited to study at school, and in accordance with this he devotes a chapter to the measurement of edaphic factors and another one to the study of soil communities. The next three chapters are devoted to the study of habitats, terrestrial, freshwater, seashore and estuarine; these seem to me excellent, full of ideas and illustrated often by actual results obtained with boys at Winchester College. The average teacher has difficulty in thinking out suitable projects for a class, or for a clever individual pupil, and he will get plenty of inspiration and suggestions here. The final chapter entitled Field Work Procedure contains much sound advice which I would recommend strongly to anyone starting to organize class field work.

An essential part of the book are the many plates and text-figures which are of a high quality. I must, however, grumble at the lines of scale alongside some of the freshwater animals which are figured. Thus in Fig. 59 the maximum size shown for *Lymnaea peregra* is too small, while that for *Eudontus* is larger than I have ever met; this applies also in Fig. 60 to *Glossiphonia*, whose name should now be *Glossiphonia*. There is a bibliography of six pages, of which half are devoted to the identification of animals. Admittedly this part is not intended in any way to be complete but I found the selection disappointing. It seems a pity, for example, that room could not be found to give the titles of some of the Scientific Publications of the Freshwater Biological Association, instead of just a general reference to the series, when there are six references for butterflies and moths. These are, however, minor points in an admirable book.

P. F. HOLMES

TWO NEW JOURNALS

Current Bibiliography for Aquatic Sciences and Fisheries edited by F.A.O. Fisheries Biology Branch. London: Taylor & Francis. Price 17*s.* 6*d.* per part or £9 per volume (12 parts).

F.A.O. began in 1958 to issue monthly from its office in Rome a mimeographed 'Current Bibliography for Fisheries Science' so arranged that it could be cut up to yield entries on card index cards. This was distributed free of charge to research institutes and libraries many of which gave assistance in its compilation. The circulation has now become too large for such methods to be suitable, and beginning with Vol. 3 (1960) it is to be printed and distributed as an abstracting journal at the prices shown above.

Russian Review of Biology translated from УСПЕХИ СОВРЕМЕННОЙ БИОЛОГИЙ. London and Edinburgh: Oliver & Boyd. Price £9 for the first nine issues (Vol. 48 (1) (2) (3) of 1959 and six issues for 1960); thereafter £6 10*s.* a year.

This translation direct from the Russian journal results from collaboration between the Institute of Biology and the Department of Scientific and Industrial Research. The first issue (Vol. 48, No. 1) contains an editorial article, five papers reporting the results of original research, and one, headed *Current Events* in the list of contents, which might be called scientific journalism. In the first paper Prof. A. N. Studitskii (Deputy Editor) writes what is in effect a longish essay-review of Lenin's book *Materialism and Empirio-Criticism* (1909) in which he attacked the bourgeois philosophy of Mach and his followers Bazarov, Bogdanov and Lunacharskii; the next five papers are all biochemical or immunological; the last, by Kh.S. Koshtoyants, bears the title 'The work of Cambridge biologists', but as the author admits, it is far from being a complete account. More than half of it deals with work in progress in the Department of Zoology, but there are also brief references to the Departments of Physiology, Radiotherapy and Anatomy and to the Medical Research Council's Unit for Molecular Biology in the Cavendish Laboratory.

The journal is well produced, but it is surprising to find no text-figures. In three papers the reference lists are in two parts: Russian and non-Russian. In two of these the non-Russian list much exceeds the Russian; in the third they are about equal.

BOOKS RECEIVED

Africa's Wild Glory by W. Philip Keller. London: Jarrold. 1959. Price 35*s.*

Ciba Foundation Colloquia on Ageing. Vol. 5. *The lifespan of animals* ed. G. E. W. Wolstenholme & Maeve O'Connor. London: Churchill. 1959. Price 48*s.*

Annales Instituti Biologici (*Tihany*) *Hungaricae Academiae Scientiarum* (*Annal. Biol. Tihany*) Vol. XXXVI, ed. B. Entz. Tihany. 1959.

Exploration du Parc National Albert Fasc. 1. *Introduction à l'Écologie des Ongulés* by François Bourlière & Jacques Verschuren. Brussels: Inst. Parcs Nat. Congo Belgi. 1960. (No price given.)

The Road to Man by Herbert Wendt, translated by Helen Sebba. London: Lutterworth Press. 1960. Price 30*s.*

Wildlife of Mexico: the game birds and mammals by A. Starker Leopold. Berkeley: Univ. Calif. Press (London: Cambridge Univ. Press). 1960. Price 100*s.* ($12.50).

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Hawks and Owls: population trends from Illinois Christmas counts by Richard R. Graber & Jack S. Golden. Urbana, Ill.: Biol. Notes Ill. Nat. Hist. Survey, No. 41. 1960. (No charge.)

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Proceedings of the New Zealand Ecological Society, No. 7. Wellington: N.Z. Ecol. Soc., Box 202. 1960. Price 7*s.* 6*d.*

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An Introduction to Animal Physiology by W. B. Yapp, second edition. Oxford: Clarendon Press. 1960. Price 25*s.*

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, F. A. O. Fisheries Division, P. D. Gabbutt, D. Leatherdale, A. Macfadyen, J. M. D. Mackenzie, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, C. D. Putnam, Mrs M. Vincent, and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

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CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

	PAGE
1. Ecological surveys and the relations of animals to habitat conditions	412
(*a*) Marine and brackish	412
(*b*) Fresh water	413
(*c*) Land	414
2. Methods, apparatus, population statistics and taxonomic studies of use to ecologists	418
3. Parasites	420
4. Food and food habits	420
5. Migration, introductions and local distribution	421
6. Studies on behaviour	425
7. Reports of organizations	426

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Cole, H. A. & Waugh, C. D. (1959). The problem of stunted growth in oysters. *J. Cons. Int. Explor. Mer,* **24,** 355-365.

Analyses effects of low temperature, food shortage, water borne mineral particles, infestation with *Polydora,* shell disease and culture methods on stunting of *Ostrea edulis* on British coasts.

Crisp, D. J. & Ryland, J. S. (1959). Influence of filming and of surface texture on the settlement of marine organisms. *Nature, Lond.* **184,** 119.

A well cleaned surface allowed to stand in sea water becomes coated with a film which thickens for at least a few days. The assumption that this film is a necessary prerequisite to the settlement of marine larvae and that a roughened surface is more suitable are being tested. Preliminary results involving various species indicate that neither of the generalities is valid. There is a considerable diversity in behaviour towards the films.

Forster, G. R. (1959). The ecology of *Echinus esculentus* L. Quantitative distribution and rate of feeding. *J. Mar. Biol. Ass. U.K.* **38,** 361-367.

Underwater counting reveals a density of up to 868 urchins per acre. By browsing on algae and sessile animals an abundant population can clear at least one-third of the rock surface per annum.

Gibson, F. A. (1959). Some observations on the occurrence of *Leander serratus* Pennant in Irish waters. *J. Cons. Int. Explor. Mer,* **24,** 349-354.

Discusses creel catches of prawns in relation to abundance of shore crabs and distribution of *Zostera,* and analyses size and maturity in catches.

Gibson, F. A. (1959). Notes on the escallop (*Pecten maximus* L.) in three closely associated bays in the west of Ireland. *J. Cons. Int. Explor. Mer,* **24,** 366-371.

Compares growth and maturation in three populations and suggests means of improving stocks.

Haderlie, E. C. & Clark, R. B. (1959). Studies on the biology of the Bristol Channel XIX. Notes on the intertidal fauna of some sandy and muddy beaches in the Bristol Channel and Severn estuary. *Proc. Bristol Nat. Soc.* **29** (5), 459-468.

Divides the Bristol Channel and Severn estuary into marine, transition and estuarine zones on the basis of salinity and deposition of silt, and discusses in particular the distribution of species of *Nephtys* in the region.

Hewer, H. R. & Backhouse, K. M. (1959). Field identification of bulls and cows of the grey seal, *Halichoerus grypus* Fab. *Proc. Zool. Soc. Lond.* **132,** 641-645.

Uses colour tones on head, neck, belly and flippers; based on observations of British colonies.

Houghton, D. R. & Millar, R. H. (1960). Spread of the ascidian, *Styela mammiculata* Carlisle. *Nature, Lond.* **185,** 862.

This new species was first taken in 1953 near Plymouth. The discovery of numerous specimens in Langston Harbour, Hampshire, is therefore of interest. The species seems to be spreading its range rapidly along the south coast of England.

Howie, D. I. D. (1959). The spawning of *Arenicola marina* (L.). *J. Mar. Biol. Ass. U.K.* **38,** 395-406.

Regional analysis of environmental variations in the breeding season over England, Scotland and Ireland.

Mauchline, J. (1959). The development of the Euphausiacea (Crustacea) especially that of *Meganyctiphanes norvegica. Proc. Zool. Soc. Lond.* **132,** 627-639.

Reviews, discussing nomenclature of larvae, based on a study of samples from the Clyde sea area

Menzies, R. J. (1959). *Priapulus abyssorum*, New Species, the first abyssal priapulid. *Nature, Lond.* **184,** 1585-1586.

Obtained from a depth of 5680-5690 m at the southern end of the mid-America Trench. the specimen is a 'missing link' in what was considered a classic case of bipolar distribution. A description of the species is given.

Morton, J. E. (1959). The habits and feeding organs of *Dentalium entalis*. *J. Mar. Biol. Ass. U.K.* **38,** 225-238.

Describes the habitat, burrowing in medium to coarse sand, and capture of foraminiferan food by means of tentacles.

Ottestad, P. (1960). Forecasting the annual yield in sea fisheries. *Nature, Lond.* **185,** 183.

It has been suggested that it might be possible to compute yield forecasts by means of an aggregate of sine functions, using the periodic or period-like fluctuations found in growth rings of forest trees. The annual yields of the skrei fisheries (1885-1939) are compared with measurements of growth in the Scots Pine. A forecast of the post 1939 years agrees closely with the observed catches. A improved technique might prove valuable to other fisheries.

Ryland, J. S. & Austin, A. P. (1960). Three species of Kamptozoa new to Britain. *Proc. Zool. Soc. Lond.* **133,** 423-433.

Two of these, which are normally epizoic, were found on test surfaces in a warm dock; one was known before from the Red Sea and Eastern Mediterranean, the other from the Arctic. The first settles in the summer and the latter in the winter to early summer.

Saundby, R. P. (1960). Observations on the grey seal at St Kilda in winter. *Proc. Zool. Soc. Lond.* **133,** 487-490.

Breeding is recorded for October and November.

Thomas, H. J. (1959). Creel selectivity in the capture of lobsters and crabs. *J. Cons. Int. Explor. Mer,* **24,** 342-348.

Discusses efficiency of different patterns of traps for *Cancer* and *Homarus* in Scottish waters. with analyses of interpretations of catch samples.

(*b*) Freshwater

Ford, J. B. (1959). A study of larval growth, the number of instars and sexual differentiation in the Chironomidae (Diptera). *Proc. R. Ent. Soc. Lond.* (A), **34,** 151-160.

Results confirm that four instars occur in each of *Prodiamesa olivacea, Clinotanypus nervosus Anatopynia trifascipennis, Procladius choreus, Cricotopus obtexens* and *Corynoneura scutellata*. In general, growth conforms to Dyar's rule except in the case of *C. obtexens* and possibly in the related *C. sylvestris*. The first four species with relatively large full-grown larvae have the highest growth rates and the bimodal frequency distribution suggests a differentiation of the sexes at this stage. The remaining species have smaller larvae, lower growth rates and show no evidence of sexual differentiation.

Frost, W. E. & Kipling, C. (1959). The determination of the age and growth of pike (*Esox lucius* L.) from scales and opercular bones. *J. Cons. Int. Explor. Mer,* **24,** 314-341.

Compares methods of estimating age and tests validity by tagging fish.

Hanna, H. M. (1959). The growth of larvae and their cases and the life-cycles of five species of caddis flies (Trichoptera). *Proc. R. Ent. Soc. Lond.* (A), **34,** 121-129.

Limnephilus flavicornis (F.), *L. lunatus* Curtis, *Potamophylax stellatus* (Curtis), *Brachycentrus subnubilus* Curtis and *Agapetus fuscipes* Curtis were studied. The increase in the size of the case was shown to parallel the growth of the larva. The life cycle of the first four species lasts one year and there is only one generation.

Hawkes, H. A. (1959). The effects of methods of sewage application on the ecology of bacteria beds. *Ann. Appl. Biol.* **47,** 339-349.

A study of the relationships between fly larvae (*Anisopus fenestralis* and *Psychoda* sp.) and a Collembolan (*Achorutes subviaticus*) under different sewage flow systems in bacteria beds.

Hynes, H. B. N. (1958). The effect of drought on the fauna of a small mountain stream in Wales. *Verh. Int. Ver. Limnol.* **13,** 826-833.

Kemp-Turnbull, P.St. (1960). Quantitative estimations of populations of the river crab *Potamon* (*Potamonautes*) *perlatus* (M. Edw.), in Rhodesian trout streams. *Nature, Lond.* **185,** 481.

Funnel mouthed traps are used in a screened but typical section of the river and since the number of animals captured declines with time the population estimate method of De Lury is applicable. In this the number of animals caught is compared with total catch to date. Extrapolation of the fitted straight line gives an estimate of the population at commencement of trapping.

Twomey, E. (1958). Fertilization of some acid or bog lakes in Ireland. *Rep. Sea Inland Fish. Ireland* **(1956),** 90-104.

Discusses the effects on plankton production and on the growth and condition of *Salmo trutta* of applications of limestone, potash and superphosphate to such acid waters.

(*c*) Land

Aldhous, J. R. (1959). Control of cutworm in forest nurseries. *Forestry,* **32** (2), 155-165.

Larvae of the moths *Agrostis segetum, Tryphena pronuba, Agrostis exclamationis,* and sometimes *Euxoa* (*Agrostis*) *nigricans, Hepialus humuli* and *H. lupulinus.* Here *A. segetum* is mainly concerned. Control by dieldrin or aldrin sprays, applied from mid-June to mid-July.

Ash, J. S. (1959). Pollen contamination of birds. *Brit. Birds,* **52,** 424-426.

Migrant warblers trapped at Portland Bird Observatory, Dorset, in spring in 1957 and 1959 had hard rubbery nodules of *Citrus* pollen adhering to their bills.

Atkinson, R. J. C. (1957). Worms and weathering. *Antiquity,* **31,** 219-233.

A detailed discussion, in the light of recent archaeological experience, of the influence of earthworms on archaeological sites and on the interpretation of the evidence. The conclusion is that some significant finds have been displaced downwards from their original position, sometimes to an extent sufficient to alter the apparent stratigraphic relationships of the objects.

Boyd, H. (1959). The composition of goose populations. *Ibis,* **101,** 441-445.

Examples of work done and in progress on the proportion of juveniles in goose flocks wintering in Britain.

Butler, C. G. (1959). The source of the substance produced by a queen honey-bee (*Apis mellifera* L.) which inhibits development of the ovaries of the workers of her colony. *Proc. R. Ent. Soc. Lond.* (A), **34,** 137-138.

The contents of the mandibular gland of a mated queen honey-bee can inhibit development of the ovaries of queenless worker honey-bees.

Collingwood, C. A. & Brock, A. M. (1959). Ecology of the black currant gall mite (*Phytoptus ribis* Nal.). *J. Hort. Sci.* **34,** 176-182.

A study of the annual population cycle of *P. ribis* in 'big buds' on the black currant variety Wellington XXX at Sutton Bonnington, with particular emphasis on the migration of the Eriophyids and its relation with gall senescence.

Coulson, J. C. (1959). Observations on the Tipulidae (Diptera) of the Moor House Nature Reserve, Westmorland. *Trans. R. Ent. Soc. Lond.* **111,** 157-174.

Records sixty-six species from this reserve. Notes the larval habitats of some species and the seasonal distribution of the adults. Marked differences are recorded in the numbers, time of abundance and species composition of tipulids from peat moss and alluvial grassland.

Crooke, M. (1959). Insecticidal control of the pine looper in Great Britain. I. Aerial spraying. *Forestry,* **32** (2), 166-196.

The moth, *Bupalus piniarius,* is indigenous but is first recorded as an epidemic at Cannock Chase where over 100 acres of 31 year Scots Pine were completely defoliated in 1953. Many plantations are now reaching the vulnerable stage. A general survey was made throughout the country, and control by aerial spraying with DDT used.

Dowsett, R. J. (1960). Starlings affected by smog. *Brit. Birds*, **53,** 33.

On two foggy nights at Bishop Stortford, Hertfordshire, in January 1958, starlings were killed by asphyxia, and on a third occasion corpses were found after a clear night. (See also Peet, W. M., 1959, *Brit. Birds*, **52,** 238. Abstract in *J. Anim. Ecol.* **29,** 202).

Edwards, V. C. Wynne- (1959). The control of population-density through social behaviour: a hypothesis. *Ibis*, **101,** 436-441.

Advances a theory that population-densities are controlled by conventional substitutes, e.g. territory, rather than directly by competitition for food.

Fenwick, D. W. & Widdowson, E. (1959). The emergence of larvae from free eggs of the potato-root eelworm *Heterodera rostochiensis* (Woll.). *Ann. Appl. Biol.* **47,** 140-149.

The hatching of *H. rostochiensis* from eggs removed from presoaked cysts was found to be similar to, but quicker than, the hatching from encysted eggs.

Finnis, R. G. (1960). Road casualties among birds. *Bird Study*, **7,** 21-32.

Collates own observations near Gravesend with published and unpublished data from other areas. Casualties in France and America seem markedly less. Records high mortalities among blackbirds, thrushes and house sparrows and indicates local causes of death at gateways, sudden changes of bank level and along narrow verges. Species lists for two localities in an appendix.

Fisken, A. G. (1959). Factors affecting the spread of aphid borne viruses in potato in eastern Scotland. I. Overwintering of potato aphids, particularly *Myzus persicae* (Sulzer). *Ann. Appl. Biol.* **47,** 264-273.

Fisken, A. G. (1959). Factors affecting the spread of aphid-borne viruses in potato in eastern Scotland. II. Infestation of the potato crop by potato aphids, particularly *Myzus persicae* (Sulzer). *Ann. Appl. Biol.* **47,** 274-286.

Bionomics of the overwintering of the aphids *Myzus persicae* (Sulz.), *Macrosiphum euphorbiae* (Thom.) and *Aulacorthum solani* (Kltb.) in Scotland, mainly as apterae on perennial, glasshouse, frame and brassica crops. The market-gardens of the Lothians are an important source from which *M. persicae* disperse in the spring to colonize potato crops in eastern Scotland. The infestation of potatoes and trap records of the dispersal of the three species in 1954-56 are considered in the second paper.

Free, J. B. & Spencer-Booth, Y. (1959). The longevity of worker honey-bees (*Apis mellifera*). *Proc. R. Ent. Soc. Lond.* (A), **34,** 141-150.

The introduction of one hundred marked bees per week into four colonies from March to October shows that bees emerging in March lived five weeks and those in June about four; the weekly death rate was highest in midsummer and considerably lower in August; August and September emergences showed no correlation between age and the % which survived the following spring nor between age and their chances of survival at that time; there were marked differences in the longevity of bees of different colonies.

Geier, P. W. (1960). Physiological age of codling moth females (*Cydia pomonella* (L.)) caught in bait and light traps. *Nature, Lond.* **185,** 709.

The physiological age of females caught in these traps is compared. The light traps drew samples of significantly younger flies from the field population. When catches are recorded as a guide to the timing of spray treatment, the light traps have several advantages over bait traps.

Gifford, D. (1960). Notes on Scottish woodland insects: 2. Defoliation of newly planted conifers in Perthshire, by *Strophosomus* spp. (Coleoptera: Curculionidae). *Scot. For.* **14,** 31-33.

In one area, *S. melanogrammus* and *S. capitatus* killed nearly all Scots pine and Douglas by June in the year of planting. Corsican pine, silver fir and Norway spruce were little affected. The cause was a very thorough cleaning of all other vegetation, removing all the normal food.

Homes, R. C., Sage, B. L. & Spencer, R. (1960). Breeding population of lapwings, coot and meadow pipits. *Lond. Bird Rep.* **23** (1958), 54-61.

Four hundred and nineteen breeding pairs of coot found in the area within a 20-mile radius of St. Paul's Cathedral in 1957, mostly on lakes, ponds and flooded gravel and other pits, the highest concentration in Herts. A similar survey of lapwings indicated the presence of some 130 pairs on agricultural land and some 226 in other habitats, including sewage farms, which were preferred (44-45 pairs), and established the importance of a damp environment in the breeding area. Building operations, drainage and flooding of the Thames marshes have contributed to a decline in breeding populations. About 80 pairs of meadow pipits occurred in the area, mostly in heath or waterside habitats, and 26 pairs are known to have bred or attempted to breed. From about the beginning of October, the birds left the heaths. Numbers increased considerably during winter, the highest concentrations (100-300) being on sewage farms, ploughed land and riverside marshes.

Hunter-Jones, P. & Ward, V. K. (1959). The life-history of *Gastrimargus africanus* Saussure (Orth. Acrididae) in the laboratory. *Ent. Mon. Mag.* **95,** 169-172.

Jepson, W. F. & Heard, A. J. (1959). The frit fly and allied stem-boring Diptera in winter wheat and host grasses. *Ann. Appl. Biol.* **47,** 114-130.

Food-plant preferences of species of *Oscinella, Meromyza* and *Opomyza* on ley plots of *Lolium perenne, Dactylis glomerata, Festuca arundinacea, F. rubra, Agrostis tenuis* and *Poa pratensis* in Berkshire. Larval populations on the leys were reflected in the populations in winter wheat which followed the ploughing-up of the leys.

Kent, N. L. (1959). Contamination of stacked grain by rats and mice. *Scot. Agric.* **39,** 98-101.

Data are provided on the degree of infestation of stacked wheat in Scotland by rats and mice, measured by the number of excreta pellets per 10 lb.

Lines, R. (1960). Common silver fir in Britain. *Scot. For.* **14,** 20-30.

About 1920, *Abies alba* ceased to be planted in Britain as a forest tree because of damage by *Adelges* spp. Various forms of the insect are discussed, especially their effects on trees of different provenances and even on individual trees which seem to be resistant. It may be possible to plant selected strains in Britain.

McVean, D. N. (1959). Muir burning and conservation. *Scot. Agric.* **39,** 79-82.

Although the burning of moors generally results in more sheep and grouse to the acre, attention is drawn to the ill effects of the practice in physical damage to the soil, chemical loss and the invasion of undesirable plants. A code of practice for the burning of heather is suggested.

Marshall, A. J. (1959). Internal and environmental control of breeding. *Ibis,* **101,** 456-478.

The rhythm of reproduction in seasonal birds is at first endogenous, but later influenced by external, including immediate environmental factors.

Milne, B. S. (1959). Variation in a population of yellow wagtails. *Brit. Birds,* **52,** 281-295.

Three seasons' observations of a colony of yellow wagtails suggest that yellow-headed and grey-headed birds are specifically distinct, and that hybridization occurs. Males resembling *Motacilla flava beema* in populations in southern England are probably not that race since no females are recorded.

Mutchmor, J. A. & Mazurek, M. (1959). Chemical changes associated with diapause in the european corn-borer, *Orstrinia nubialis* (Hbn.), (Lepidoptera: Pyralidae). *Nature, Lond.* **184,** 1077-1078.

Induction of diapause at 65° F requires that the last larval instar be exposed to photoperiods of 9.5-14 hours per day for about three weeks. The differences in amino-acid composition between diapause and non-diapause borers is discussed as revealed by two-dimensional chromatography. Details of the methods employed are given. An unidentified peptide was present in those borers not in diapause. Secondly, these larvae had a lower concentration of proline than those in diapause.

Orford, N. W. (1959). An unusual breeding habitat of the linnet. *Nature, Lond.* **84,** 650.

The species has been nesting annually in clumps of rushes in north-east Cheshire.

Phillips, J. (1960). Ecology in Africa: from the Sudan to Transvaal. *Discovery,* **21,** 116-120.

Underlines the need for ecological studies if the development of natural resources in Africa south of the Sahara is to be accomplished with maximum efficiency.

Phillipson, J. (1959). The seasonal occurrence, life histories and fecundity of harvest-spiders (Phalangida, Arachnida) in the neighbourhood of Durham City. *Ent. Mon. Mag.* **95,** 134-138.

A study of ten species of harvest-spiders from 1954 to spring 1959; with records of seasonal distribution of species, life-histories and estimates of average number of eggs per female for 1958.

Pitcher, R. S. (1959). The chemical control of leaf and bud eelworms (*Aphelenchoides* spp.) and stem and bulb eelworm (*Ditylenchus dipsaci*) on strawberries. *J. Hort. Sci.* **34,** 61-71.

In the discussion to this paper, three factors (acting together or separately) are considered of importance in determining the rate of increase of nematodes in strawberries. They are: spread amongst strawberry plants; spread from weeds to strawberries; and an increase of the nematode population of individual strawberry plants to or beyond the level at which symptoms appear.

Ratcliffe, D. A. (1960). Broken eggs in the nests of sparrowhawk and golden eagle. *Brit. Birds,* **53,** 128-130.

Eggs were broken or disappeared in eight sparrowhawk nests, chiefly in the latter half of the period 1943-1959 when several regular territories near Carlisle were deserted. Similar breakages were observed in golden eagle eyries but not in nests of other raptors except peregrine. (See 1958, *Brit. Birds,* **51,** 23-26 and abstract in 1958, *J. Anim. Ecol.* **27,** 416).

Shanks, P. L. (1959). Ragwort in silage. *Scot. Agric.* **39,** 103-104.

Ragwort is increasing owing to the lack of control by rabbits, and its ingestion probably causes a higher mortality of British livestock than all other poisonous plants together. Herbicides render the plant more appetising to cattle, and it is inseparable in silage.

Sharman, A. (1959). Muscular distrophy of calves: a recent advance. *Scot. Agric.* **39,** 69-70.

Muscular distrophy, which may occur when indoor-suckled calves are first turned out to grass in the spring, is associated with vitamin E deficiency and with selenium deficiency in the soil.

Smith, D. Summers- (1959). The house sparrow *Passer domesticus*: population problems. *Ibis,* **101,** 449-454.

Examines the influence of habitat on numbers and the seasonal variation in a population. The house sparrow population of Great Britain is estimated at 10 millions: censuses in different parts of its range suggest a ratio of 1 : 5 of human population.

Southern, H. N. (1959). Mortality and population. *Ibis,* **101,** 429-436.

Mortality is considered the important factor controlling populations. The breeding success of a tawny owl population was closely linked with the abundance of rodents year by year. Such density-dependent mortality may be widespread in bird populations.

Wallace, H. R. (1959). The movement of eelworms in water films. *Ann. Appl. Biol.* **47,** 366-370.

The relative movements of the nematodes *Aphelenchoides ritzemabosi* and *Heterodera schachtii* in thick and thin water films.

Wallace, H. R. (1959). Movement of eelworms. IV. The influence of water percolation. *Ann. Appl. Biol.* **47,** 131-139.

Experimental findings on the relationship between the rate of water flow through sands of different particle sizes and the downward velocity of the nematodes *Heterodera rostochiensis, Ditylenchus dipsaci, Panagrolaimus rigidus, Panagrellus redivivus* and *Diplogaster lheritieri.*

Wallace, H. R. (1959). Movement of eelworms. V. Observations on *Aphelenchoides ritzema-bosi* (Schwartz, 1912) Steiner, 1932 on florists' chrysanthemums. *Ann. Appl. Biol.* **47,** 350-360.

Nematode activity on chrysanthemums in relation to the presence of water films. Leaves were observed to be invaded via the stomata, and activity within the plant is also considered.

Way, M. J. (1959). The effect of temperature, particularly during diapause, on the development of the egg of *Leptohylemyia coarctata* Fallén (Diptera: Muscidae). *Trans. R. Ent. Soc. Lond.* **111,** 351-364.

Details lower and upper limits for the different stages of development. The optimum constant temperature for diapause development in 3° C and the egg can develop through all stages at an optimum of about 7° C. It is suggested that the temperature optimum for diapause may vary as development proceeds.

Zaher, M. A. & Long, D. B. (1959). Some effects of larval population density on the biology of *Pieris brassicae* L. and *Plusia gamma* L. *Proc. R. Ent. Soc. Lond.* (A), **34,** 97-109.

The abnormal condition of experimental crowding of *P. gamma* shortens the larval duration, prolongs the pupal period, reduces the preoviposition period and increases the numbers of eggs laid. In *P. brassicae* the abnormal condition of isolation prolongs the larval and pupal periods, shortens the pre-oviposition period but increases the number of eggs laid.

It is suggested that these dependent series of effects constitute a compensatory response to abnormal population densities.

Zahar, M. A. & Moussa, M. A. (1959). Relationship between larval and pupal periods of some lepidopterous insects. *Nature, Lond.* **184,** 288.

Parallel cultures of *Plusia gamma* and *Prodenia litura* were maintained in solitary and crowded conditions. A negative relationship exists between the durations of larval and pupal periods. Also, the larval period was longer in solitary culture.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Bailey, R. (1960). Description of the female of *Meraporus tenuicornis* Graham and its habitat, with a brief redescription of *M. graminicola* Walker (Hym. Pteromalidae). *Entomologist,* 40-43.

Larvae of *M. tenuicornis,* the female of which was hitherto unknown, were found in small swellings on the stem internodes and leaf sheaths of *Agropyron repens,* where they are parasitic on *Tetramesia linearis* and its parasite, *Eurytoma flavimana.* Of 98 galls on 20 stems found in Lancashire, 60 contained *T. linearis,* 28 *E. flavimana* and 10 *M. tenuicornis*; of the last, six were females. In Leicestershire, 2 of 167 galls contained *M. tenuicornis,* both females

Brinkhurst, R. O. (1959). A description of the nymphs of British *Gerris* species (Hemiptera-Heteroptera). *Proc. R. Ent. Soc. Lond.* (A), **34,** 130-136.

Includes a key to the fourth and fifth instar nymphs of the nine British species.

China, W. E. & Miller, N. C. E. (1959). Check-list and keys to the families and subfamilies of the Hemiptera-Heteroptera. *Bull. Brit. Mus. Nat. Hist. (Ent.),* **8,** (1) 1-45.

Covers British families and sub-families.

Clay, T. (1959). Key to the species of *Austromenopon* Bedford (Mallophaga) parasitic on the Charadriiformes. *Proc. R. Ent. Soc. Lond.* (B), **28,** 157-168.

Eales, N. B. (1960). Revision of the world species of *Aplysia* (Gastropoda, Opisthobranchia). *Bull. Brit. Mus. Nat. Hist. (Zool.),* **5** (10), 267-404.

Includes descriptions of, and notes on *A. (Pruvotaplysia) punctata,* the only truly indigenous British species and two occasionals, *A. (Varria) fasciata* and *A. (A.) depilans.*

Goodwin, D. (1959). Taxonomy of the genus *Columba*. *Bull. Brit. Mus. Nat. Hist. (Zool.)*, **6** (1), 1-23.

Fifty species, three of which are British, are grouped mainly by *basic* colour pattern and geographical distribution.

Lewis, T. (1960). A method for collecting Thysanoptera from Gramineae. *Entomologist*, **93**, 27-28.

Tillers are put into a lampglass with a polythene funnel dipping into a collecting tube containing water and a drop of detergent sealed into the narrow end and a wire basket containing cotton wool soaked in turpentine sealed to the inside of the lid. Thrips fall into the collecting tube within 30 minutes. The method was equally successful for adults of both sexes, but less so for the immature stages, especially the third and fourth instars. It appeared satisfactory for *Limothrips cerealium*, *Chirothrips manicatus* and *Stenothrips graminum* in various cereals and grasses.

McDonald, W. A. (1960). Nocturnal detection of tsetse flies in Nigeria with ultra-violet light. *Nature, Lond.* **185**, 867-868.

An apparatus is described which refines the technique of locating tsetse flies marked with fluorescent paint. Its principal advantage lies in its portability.

Milne, A., Yapp, W. B. & Varley, G. C. (1959). A controversial equation in population ecology. *Nature, Lond.* **184**, 1582-1583.

A continuation of the discussion of Nicholson's equation. Milne criticises Nicholson's theory of population control and particularly the equation. He holds that it merely shows the maximum possible population density possible with an amount of requisite which has been determined by its rate of generation and its rate of loss. Yapp points out that only rarely is there available a discrete food supply which is not added to during the life of the population, thus the use of the equation purporting to represent the conditions necessary for equilibrium is invalid. Varley replies to the criticisms.

Paramonov, A. (1959). A possible method of estimating larval numbers in tree crowns. *Ent. Mon. Mag.* **95**, 82-83.

The method has given promising results in estimating larval numbers in tree crown populations, especially with the early instars of *Bupalus pinniarius*. Head capsules, which fall on ecdysis, were collected in standard metal funnels, with replaceable muslin bags attached to the neck, supported in frames three feet from the ground.

Parrish, B. B., Baxter, I. G. & Mowat, M. J. D. (1960). An automatic fish egg counter. *Nature, Lond.* **185**, 777.

An apparatus is described which facilitates investigations into the fecundity of fish. It enables rapid counts to be made and eliminates the tedium of hand counting.

Le Quesne, W. J. (1960). Some modifications in the British list of Delphacidae (Hem.), including a new genus and a new species. *Entomologist*, **93**, 13-19, 29-35, 54-60.

This revision includes a check list of the British species, with keys and distributions for some.

Quick, H. E. (1960). British slugs (Pulmonata; Testacellidae, Arionidae, Limacidae). *Bull. Brit. Mus. Nat. Hist. (Zool.)*, **6** (3), 103-226.

Notes on external appearance, internal anatomy, behaviour, ecology and distribution (with vice-county maps) of 24 native species and 2 greenhouse aliens.

Raw, F. (1959). Estimating earthworm populations by using formalin. *Nature, Lond.* **184**, 1661-1662.

The application of formalin to light well-drained soils is discussed as a means of recovering worms and providing population estimates. The concentration of formalin applied was found to be important.

Royama, T. (1959). Test of an automatic nest-recorder. *Brit. Birds*, **52**, 295-302.

The recorder described was designed to record visits of male and female to a nest box separately, and proved satisfactory with great tits.

Salmon, J. T. (1959). Concerning the Collembola Onychiuridae. *Trans. R. Ent. Soc. Lond.* **111,** 119-156.
Includes a key to the sub-families and genera of the Onychiuridae.

Taylor, R. H. (1959). Age determination in wild rabbits. *Nature, Lond.* **184,** 1158-1159.
The fusion of epiphyses of vertebrae to the centra is suggested as an age criterion for older animals.

3. PARASITES

Askew, R. R. (1959). Some observations on *Diplolepis rosae* (L.) (Hym., Cynipidae) and its parasites. *Ent. Mon. Mag.* **95,** 191-192.

Hillis, J. P. & O'Riordan, C. E. (1960). Parasites of a sunfish, *Mola mola*, from the Irish coast. *Irish Nat. J.* **13,** 123-124.
Two species of cestode and two of copepods.

Kabata, Z. (1957). Note on a new host of *Myxobolus aeglefinis*. *Parasitology,* **47,** 165-168.
Records parasitization of the cranium of *Pleuronectes platessa*.

Kabata, Z. (1959). Ecology of the genus *Acanthochondria* Oakley (Copepoda parasitica). *J. Mar. Biol. Ass. U.K.* **38,** 249-261.
Discusses the distribution of four species of this genus of parasitic copepod in their various hosts of flatfish.

Meerovitch, E. (1960). Thermal barrier to the infectivity of *Entamoeba invadens* in snakes. *Nature, Lond.* **185,** 631.
Experiments are described which show that *E. invadens* cannot survive in grass snakes kept at temperatures above normal. The temperatures used were in the order of 34-37° C. A control snake maintained at 20-23° C developed typical amoebiasis about one week after inoculation.

Sharp, N. C. C. (1959). Husk—the development of a vaccine. *Agriculture,* **66,** 241-245.
Cows can be immunized against this disease, caused by *Dictyocaulus viviparus*, by an oral dose of X-irradiated infective larvae which pass through the hosts gut wall, producing immunity to subsequent attacks, but are not strong enough to reach the lungs where the major damage is done.

Sidor, C. (1959). Susceptibility of larvae of the large white butterfly (*Pieris brassicae* L.) to two virus diseases. *Ann. Appl. Biol.* **47,** 109-113.
Larvae of *Pieris brassicae* collected from Cambridgeshire and Hertfordshire which were most susceptible to a natural granulosis infection were also more susceptible to a cytoplasmic polyhedral virus derived from *Phalera bucephala*.

4. FOOD AND FOOD HABITS

Antoine, N. J. (1959). Blue tit feeding young treecreepers. *Brit. Birds,* **52,** 432-433.
A male blue tit fed young treecreepers but not his own young nearby, both in the nest and after fledging. He brought caterpillars, the parents moths and crane flies.

Blackett, A. (1960). Blackbird incubating and song thrush rearing combined brood. *Brit. Birds,* **53,** 89-90.
Eggs of both species were incubated by the blackbird only, but the young were reared successfully by the song thrush alone.

Bullivant, J. S. (1959). Stomach contents of spawning quinnat salmon. *Nature, Lond.* **184,** 71.
Forty-three specimens were examined, 39 of which had nothing in the stomach. Three contained younger salmon, and one parts of the aquatic plant *Potamogeton*.

Cordero, R. & Cordero, J. (1960). Robins feeding nestling blackbirds. *Brit. Birds*, **53**, 131-132.
A male robin with young near a blackbird's nest fed only the young blackbirds. When frightened at her own nest the female robin also fed the blackbirds. Both broods fledged.

Cranbrook, The Earl of (1959). The feeding habits of the water shrew, *Neomys fodiens bicolor* Shaw, in captivity and the effect of its attack upon its prey. *Proc. Zool. Soc. Lond.* **133**, 245-249.
Poison injected by biting is effective with invertebrates but not vertebrates. The idea that moles paralyse worms is discounted.

Crowcroft, P. (1959). Spatial distribution of feeding activity in the wild house-mouse (*Mus musculus* L.). *Ann. Appl. Biol.* **47**, 150-155.
In this experimental study of the feeding behaviour of the house mouse, sporadic feeding over the whole of the available feeding area was the general pattern, but new sources of food were investigated as soon as they were introduced and old sites correspondingly neglected.

Curtis, W. P. (1960). Note on *Selenia bilunaria* (Lepidoptera). *Entomologist*, **93**, 12.
A male *S. bilunaria* pursued by a robin entered the fairly dense growth of a *Pyracantha* when the bird was about 25 ft. away from it. After careful scrutiny for about two minutes from a stone some 5 ft away, the robin darted into the bush and emerged with the moth, which it swallowed.

Fisher, L. R. & Goldie, E. H. (1959). The food of *Meganyctiphanes norvegica* (M. Sars), with an assessment of the contributions of its components to the vitamin A reserves of the animal. *J. Mar. Biol. Ass. U.K.* **38**, 291-312.
Traces vitamin A and its precursors from dinoflagellates, diatoms, algae and fern sporangia, all of which are eaten by this euphausiid.

Newton, I. (1960). The diet and feeding habits of the bullfinch. *Bird Study*, **7**, 1-9.
Field observations in Derbyshire and Somerset from 1953 to 1959. The diet is of buds in spring, insects in early summer, berries in autumn and seeds in late summer and winter. Seeds of birch, ash and meadowsweet are preferred. Data on feeding habits and a species list of plants taken.

Thompson, T. E. (1959). Feeding in nudibranch larvae. *J. Mar. Biol. Ass. U.K.* **38**, 239-248.
Main observations on veligers of *Archidoris pseudoargus* with notes on twelve other species.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Aston, A. (1959). Some additions to the Suffolk Lepidoptera. *Ent. Rec.* **71**, 281-282.
Seven new county records.

Baynes, E. S. A. (1960). Report on migrant insects in Ireland for 1959. *Irish Nat. J.* **13**, 111-116.
Records of Lepidoptera only: 7 butterflies and 9 moths.

Benson, R. B. (1960). Studies in *Pontania* (Hym., Tenthredinidae). *Bull. Brit. Mus. Nat. Hist. (Ent.)* **8** (9), 367-84.
Includes notes on some British species.

Carlisle, R. W., Palmer, R. F. & Skillen, S. (1960). Natterer's bat, *Myotis nattereri* Kuhl., Castlecoole, Co. Fermanagh. *Irish Nat. J.* **13**, 121.
The second record for the county for this very local Irish bat.

Carter, W. A. C. (1960). Butterfly collecting in the Beaconsfield area. *Middle-Thames Naturalist*, **11**, 4-9.
Contains information, based on observations over 25 years, of the occurrence and numbers of butterflies of 39 species in Bucks. within 20 miles of Beaconsfield. It is suggested that the virtual disappearance of the Adonis blue (*Lysandra bellargus*) may be due to the suppression of its food-plant by rank growth following the elimination of grazing by rabbits.

O J.A.E.

Cole, J. H. (1959). Hover Flies Family Syrphidae. An introduction and interim list of Syrphidae of the Reading area. *Reading Nat.* **11,** 20-29.

Records for some 115 species and varieties from Berkshire and Oxfordshire, including at least one new one for Oxfordshire.

Cook, L. M. (1959). The distribution in Britain of the scarlet tiger moth, *Callimorpha* (*Panaxia*) *dominula* L. *Entomologist,* **92,** 232-236.

Localities from which colonies have been recorded during the past 80 years are listed and mapped. A contraction of the range from the north-east indicated over the past 30 years is the direct opposite of the change that has occurred over the same period in some other Lepidoptera.

Corbet, G. B. (1960). Wood mice at high altitude in Scotland. *Proc. Zool. Soc. Lond.* **133,** 486-487.

Wood mice at high altitude in Scotland. Two large specimens.

Cornwallis, R. K. (1959). Bird Observatories. *Ibis.* **101,** 424-427.

An assessment of research on migration at British Bird Observatories and suggestions for future work.

Cramp, S. (1960). The irruption of tits and other species in the London area, 1957-1958. *Lond. Bird Rep.* **23** (1958), 62-69.

The irruption of blue tits, with considerably smaller numbers of great and coal tits, in the autumn of 1957 was on a considerable scale in this area, and there was some evidence of return movements, mainly of blue and great tits, in early 1958. Opening of milk bottles and attacks on paper, putty, etc., were also on an increased scale. Counts of tits in Central London provided a valuable index of the size and nature of the irruption, and ringed birds were recovered at distances up to four times greater than usual. Movements of jays were also on an unusual scale, and there were some increases in numbers of nuthatches, long-tailed tits, hedge-sparrows and, to a less extent, wrens, tree-creepers and goldcrests. There appeared to be no marked increase in the number of tits breeding in 1958, but nuthatches bred in Central London for the first time this century.

Delany, M. J. & Copland, W. O. (1960). The mammals of the island of South Rona. *Proc. Zool. Soc. Lond.* **133,** 483-486.

A list of small mammals trapped.

Duncan, C. J. (1960). The grasshoppers of Skokholm Island, Pembs. *Entomologist,* **93,** 25-26.

Chorthippus brunneus and *Omocestus viridulus* are the two species represented, but since, owing to heavy grazing by rabbits and sheep and the effects of spray, the grassland habitat provides little cover from insectivorous birds, they occur almost entirely in marsh and bracken habitats, where there is both cover and a food supply. A few were also found in stunted heather and in sheltered patches of *Silene maritima.*

Elton, C. S. (1959). Swarming of male *Culex pipiens* L. (Dipt., Culicidae). *Ent. Mon. Mag.* **95,** 189-190.

Large swarms of male *Culex pipiens* were observed from a top floor flat in North Oxford from July to November. The swarms occurred in the same places each evening.

Harper, G. W. (1960). The Macrolepidoptera of Inverness-shire: Newtonmore district. Supplement No. 5. *Ent. Rec.* **72,** 14-15.

Records of three species new to the district.

Harris, M. P. (1959). The status of the eider (*Somateria mollissima*) in Wales. *Nature in Wales,* **5,** 849-852.

The eider is only a rare visitor to most coastal counties of Wales and was most common in 1957 and 1958. In the Burry estuary it is seen regularly.

Healy, A. (1958). Roach and dace in the Cork Blackwater. *Rep. Sea Inland Fish. Ireland* **(1956),** 67-78.

Discusses the growth and feeding of these two fish during 1956.

Hickling, R. A. O. (1960). The coastal roosting of gulls in England and Wales 1955-56. *Bird Study*, **7**, 32-52.

Records winter survey, by BTO questionnaire, of 120 roosts with county distribution. Average size of roost 7500, general range 1000 to 35 000, total population 500 000. Proportions of common species are estimated in 98 roosts. Details in appendix.

Home, W. M. Logan *et al.* **(1958).** Ornithological and other notes. *Hist. Berwicks. Nat. Cl.* **34,** 152-154.

Includes a census of breeding sea-birds on the Berwickshire coast.

Hosny, M. M. (1959). A review of results and a complete list of Macrolepidoptera caught in two ultra-violet light traps during 24 months, at Rothamstead, Hertfordshire. *Ent. Mon. Mag.* **95,** 226-236.

Lack, D. (1959). Migration across the sea. *Ibis*, **101,** 374-399.

Problems of distances covered, coasting, and drift are discussed, and future work suggested.

Lane, C. & Rothschild, M. (1960). Meadow browns (*Maniola jurtina* (L.)) and whites (*Pieris* spp.) crossing a main road. *Entomologist*, **93,** 9-12.

Between 21 June and 12 July 1959, *Pieris* spp. and *Maniola jurtina* were observed to cross a main road, sometimes with heavy traffic, on fine sunny days but not on dull or wet ones. The direction of crossing in both morning and evening appeared to be at random and irrespective of wind direction. Crossing by *Maniola* reached a peak between mid-day and 2 p.m. and by *Pieris* spp. after 4 p.m. The possible significance of the movement is discussed.

Lawrence, P. N. (1960). The discovery of *Onychiurus schoetti* (Lie-Pettersen, 1896), *sensu* Stach, 1947 (Collembola) in British Caves. *Entomologist*, **93,** 36-39.

Recorded from four localities in Yorkshire, and one each in Somerset and Sutherland.

Leatherdale, D. (1959). An annotated list of gall mites (Acarina: Eriophyidae) occurring in central Berkshire and south Oxfordshire. *Reading Nat.* **11,** 30-33.

Food-plants, localities and indications of abundance for 31 species.

Long, A. G. (1958). The Macro-Lepidoptera of Berwickshire Part I. *Hist. Berwicks. Nat. Cl.* **34,** 128-51.

A detailed list of records of the butterflies of the county, including notes on habitat.

McMillen, N. (1960). The molluscan fauna of a small islet (The Island, Greenisland, Co. Antrim). *Irish Nat. J.* **13,** 124.

Seven species of terrestrial Mollusca from a small islet in Belfast Lough.

Matheson, C. (1958). Notes on the Mammals of Brecknock. *Brycheiniog J. Brecknock Soc.* **4,** 73-90.

A general account of the mammalian life of the county, with particular reference to the chief changes since the last published account of the mammals of Breconshire half a century ago. Discusses the spread of the Grey Squirrel, and the Vole plague of 1956-57.

Matheson, C. (1960). Additional gamebook records of partridges in Wales. *Brit. Birds*, **53,** 81-84.

Gives records from the gamebooks of Stackpole Court estate, Pembrokeshire, from 1823 to 1938, and compares peaks with other Welsh records. (See also 1956, *Brit. Birds*, **49,** 112-114 and 1957, ibid. **50,** 534-536. Abstracts 1956, *J. Anim. Ecol.* **25,** 444 and 1957, ibid. **27,** 424.)

Miller, P. J. (1959). *Acanthocottus lilljeborgi* (Collett) in British seas. *Nature, Lond.* **184,** 1162.

The Norway bullhead is recorded off the south coast of the Isle of Man from depths of 15-28 fathoms. The wide distribution of the fish and evidence of breeding suggests that the species is established in the Irish Sea.

Mirams, D. R. (1959). Urban bird survey. *W. Midland Bird Rep.* **25,** 8-11.

Results of a survey of the birds of the city of Birmingham in 1956; 72 species were seen.

Morgan, N. C. & Waddell, A. B. (1960). Chironomidae (Diptera) new to Perthshire including some species new to Britain. *Entomologist*, **93,** 62-69.

An annotated list, indicating abundance and distribution in Britain for 100 species, of which three are new to the British Isles, 30 new to Scotland and 60 new to Perthshire.

O'Rourke, F. (1960). More passengers on the Gulf Stream. *Irish Nat. J.* **13,** 122.

Velella velella and *Mola mola* in Co. Cork, July 1959.

Parker, A. C. (1960). Black redstarts in Inner London, 1956-1957. *Lond. Bird Rep.* **23** (1958), 74-75.

Despite demolition and rebuilding operations in the bombed areas of Cripplegate, the black redstart maintained its status and numbers during 1956-57. Nest sites and the distance flown to the feeding areas were adapted to the changing conditions.

Patil, A. M. (1958). The occurrence of a male of the prosobranch *Potamopyrgus jenkinsi* (Smith) var. *carinata* Marshall in the Thames at Sonning, Berkshire. *Ann. Mag. Nat. Hist.* (13), **1** (3), 232-240.

The first report of a male, with full description.

Peacock, J. (1959). *Cucullia absinthii* in Derbyshire. *Entomologist*, **92,** 243.

Larvae of this moth, hitherto thought to be confined to the south coast of England, were found in Derbyshire in August 1959.

Powell, H. T. (1960). *Elminius modestus* Darwin on the Isle of Cumbrae (Firth of Clyde). *Nature, Lond.* **185,** 119-120.

An additional record of this crustacean on the Isle, about 525 m north-east of previous finds.

Price, A. (1959). The Hydradephaga (Col) of the Reading district of Berkshire. *Ent. Rec.* **71,** 292-294.

A list of species taken during 1957-59, with localities, habitats and indications of abundance.

Price, A. (1959). The Hydradephaga of the Kidwelly district of Carmarthenshire: an interim report. *Nature in Wales*, **5,** 843-849.

A list of species with notes on the various habitats. The list includes *Agabus conspersus* Marsham from Ferryside, a species only once before found in Wales.

Price, A. (1960). Pond dipping in winter. *Reading Nat.* **12,** 22-26.

Observations on invertebrates in ice-covered ponds and ditches in Berks. and Carmarths., including lists of active beetles, molluscs and leeches.

Ruttledge, R. F. (1960). The crossbill invasion of 1958 and 1959. *Irish Nat. J.* **13,** 116-118.

Crossbills remained in Ireland through the winter of 1958-59, but there appears to have been a small fresh invasion in the summer of 1959. Breeding was suspected but never proved in more than one county.

Sage, B. L. (1960). The spring migration of the common gull through the London area. *Lond. Bird Rep.* **23** (1958), 69-74.

Observations on the spring movements of common gulls in the London area are discussed in relation to those in neighbouring counties. Dispersal of the wintering population is preceded and accompanied by a large-scale influx from the south during February-April. Both immigrant and wintering birds feed in Herts. to the north of the winter roosts, and evening southerly flights back to these roosts by resting immigrant birds overlap with and confuse the general northerly migration. Large open fields on chalk in north Herts. and south Cambs. are favoured as sites for resting and feeding over prolonged periods during migration.

Spencer, R. (1959). Progress and prospects in ringing. *Ibis*, **101,** 416-424.

A survey of the results of 50 years of ringing and suggestions for future work.

Sutton, S. L. (1959). Insect migration at Portland, Dorset in 1958. *Entomologist*, **92,** 257-263.

A summary of migration, mostly in Rhopalocera but including a note on Syrphids and Odonata, recorded during 1958.

Twomey, E. (1958). Salmon of the River Moy. *Rep. Sea Inland Fish. Ireland* **(1956),** 79-89.

Age, sex and size composition of *Salmo salar* in the R. Moy.

Venables, U. M. & Venables, L. S. V. (1960). A seal survey of Northern Ireland 1956-1957. *Proc. zool. Soc. Lond.* **133,** 490-494.

Shooting by salmon netters is thought to restrict numbers.

Went, A. E. J. (1960). Rare fishes taken in Irish waters in 1959. *Irish Nat. J.* **13,** 105-107.

Records of *Pristiurus melanostomus, Box boops, Cepola rubescens, Raniceps raninus, Trachinus draco, Balistes capriscus* and *Mola mola.*

6. STUDIES ON BEHAVIOUR

Bennett, C. G. & King, B. (1959). Communal bathing by black terns in deep water. *Brit. Birds*, **52,** 313-314.

Groups of thirty or more black terns swooped down and bathed in compact rafts at Chew Valley reservoir, Somerset, in hot sultry weather.

Campbell, B. (1959). Attachment of pied flycatchers *Muscicapa hypoleuca* to nest-sites. *Ibis*, **101,** 445-448.

A study from 1947 to 1958 in an old oakwood in the Forest of Dean. Males and females ringed as adults returned to boxes at an average of 125 and 175 yards respectively, but nestlings showed no attachment to their birth-sites.

Cuss, J. (1960). Unusual site of hen harrier's nest. *Brit. Birds*, **53,** 84.

The nest was in marram grass on a high fixed sand dune.

Dove, R. S. (1959). Abnormal song of chiffchaff. *Brit. Birds*, **52,** 390-391.

A chiffchaff with a song lasting up to five seconds, clearer and more decisive than normal, sang for 17 days in April without being heard in normal song.

Dyte, C. E. (1959). Some interesting habits of larval Dolichopodidae (Diptera). *Ent. Mon. Mag.* **95,** 139-143.

A survey of some of the habitats in which Dolichopodid larvae are found, with comments on variations in form and behaviour found among them.

Forges, G. des (1959). Two robins laying in one nest. *Brit. Birds*, **52,** 390.

Two eggs a day were laid, and two robins incubated without animosity. They sat at least 25 days and then deserted.

Kramer, G. (1959). Recent experiments on bird orientation. *Ibis*, **101,** 399-416.

Describes experiments with domestic pigeons and assumes the same homing ability in wild birds. (See also 1952, *Ibis*, **94,** 265-285 and 1957, ibid. **99,** 196-227, Abstracts in 1955, *J. Anim. Ecol.* **24,** 496 and 1958, ibid. **27,** 189).

Lawton, J. (1959). Greenfinches building in old nests of other species. *Brit. Birds*, **52,** 433-434.

Describes three nests adapted in different ways.

Muir, R. C. (1959). Goldfinches undoing tie-on labels and using them as nest-material. *Brit. Birds*, **52,** 434-435.

Goldfinches at East Malling Research Station, Kent, have occasionally taken labels from the branches of fruit trees by untying them since the 1930s.

Scott, R. E. (1959). Rook nesting on the ground. *Brit. Birds*, **52,** 388.

The nest was of dry grass, reed, and wool without a foundation of sticks among rushes in a field, and had three eggs.

Simmons, K. E. L. & others (1960). Notes on anting by British passerine birds in the wild. *Brit. Birds*, **53**, 11-25.

Starlings figure in ten out of fourteen observers' notes. Ants identified as used are *Lasius niger* and *L. flavus*.

Veysey, C. M. (1960). Shelducks diving at a marsh harrier in unison. *Brit. Birds*, **53**, 127-128.

A pair of shelducks harassed a male marsh harrier for more than an hour, and then climbed above it and dived at it in unison.

Wayre, P. (1960). Starlings flying at night. *Brit. Birds*, **53**, 34-35.

On a foggy evening two large flocks of starlings on their normal flight line to roost circled a lighted building for five hours.

7. REPORTS OF ORGANIZATIONS

Alyth School Naturalists' Club (1958). Magazine and Report, 1956-1957. (W. M. Young, Alyth J.S. School, Perthshire, 1*s.* 3*d.*).

Includes notes on the vertebrates, arthropods and molluscs of the district.

Bardsey Bird and Field Observatory (1958). Bardsey Observatory 1957 Report. 44 pp.

Includes list of birds seen on the island during the year, report on bird ringing, birds killed at the lighthouse, visits to nearby islet of Ynys Gwylan-fawr, and notes on the freshwater fauna.

Birmingham and West Midland Bird Club (1959). The West Midland Bird Report No. 25, 1958. pp. 56. 6*s.*

Classified faunistic notes and migration dates for the birds of Staffordshire, Warwickshire and Worcestershire.

Cheltenham Grammar School (1958). Biology Reports, No. 2.

Contains eighteen noteworthy short papers on field work by boys, dealing with bats, badgers, small mammals, rabbits and ants, mainly in the Cheltenham district of Gloucestershire, but two on Bardsey Island, North Wales.

Dauntsey's School Natural History Society (1959). Annual Report, 1957-8 and 1958-9. 23 pp. duplicated (1*s.* 6*d.* post free from Biological Dept., Dauntsey's School, West Lavington, Devizes, Wilts.).

Includes a study of the distribution of a number of local species of woodlice in relation to humidity, observations on badgers, population studies in a cold freshwater stream, and a study of earthworm populations of clay soil and a manure heap.

Freshwater Biological Association (1959). Twenty-seventh Annual Report for the year ended 31 March 1959. pp. 86. 4*s.*

In addition to the usual sections of the Director's Report dealing with the Association's research work on invertebrates, fish and physiology, there is now one on pollution research. The Pollution Research Unit has moved from Stevenage to the Ferry House, and in consequence the zoological members of its staff have resigned so there is little to report on the zoological side.

Lincolnshire Naturalists' Trust (1959). Nature Conservation in Lincolnshire, 1958. 30 pp.

Summary of the work done on the Trust's dozen nature reserves during the year.

Lowestoft and North Suffolk Field Naturalists' Club (1959). 13th Annual Report, 1958. 32 pp.

Faunistic notes on birds (and migration), other vertebrates, and Lepidoptera.

Middle-Thames Naturalist, 11, 1958 (1959).

In addition to an annual report on local birds, includes information, based on observations over 15 years, on the status of birds of local distribution in the Ascot area by E. E. Green (pp. 10-11), and an account, based on observations over 25 years, of butterflies of 39 species that occur in Bucks. within 20 miles of Beaconsfield, by W. A. C. Carter (pp. 4-9).

Reading Naturalist, 10, 1958.

Includes annual reports on local entomology and ornithology and an interim report on the local Hydradephaga by A. Price.

Reading Naturalist, 11, 1959.

In addition to annual reports on entomology (including a new record for Berkshire in Trichoptera) and ornithology, there are local lists of Syrphids and Eriophyids and a paper including information on behaviour in a Tawny Owl nestling reared in captivity.

Reading Naturalist, 12, 1960.

In addition to annual reports on local birds and insects, includes observations on invertebrates in ice-covered ponds and ditches in Berks. and Carmarths., including lists of active beetles, molluses and leeches,, by A. Price.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1959

1958	*Income*	£ s. d.	£ s. d.
	Subscriptions receivable:		
	(*Including* Arrears and *less* Payments in Advance):		
1057	Members taking *Journal of Ecology* only	1060 12 1	
562	Members taking *Animal Ecology* only ...	605 12 3	
533	Members taking both Journals ...	631 1 7	
10	Associates	11 2 6	
		2308 8 5	
	Less: Reserve carried forward to 1960 for		
406	Part 2 of *Journal of Animal Ecology* ...	416 0 0	
		1892 8 5	
219	*Add:* Reserve brought forward from 1958 for *Journal of Animal Ecology*,		
—	Vol. 28, No. 2	406 0 0	
1975			2298 8 5
109	Interest on Investments	81 0 0	
3	Interest on Deposit Account	1 18 11	
3	Interest on Post Office Savings Account	2 15 2	
115			85 14 1
	Watson's Census Catalogue of British Lichens—Sales		15 0
	Journal of Ecology:		
	Subventions towards extra plates ...		80 0 0
	Sale of Back Issues to W. J. Johnson Inc.		1174 2 8
22	Index, Volumes 1-20—Sales less cost ...		11 2 8
	Journal of Animal Ecology:		
	Volume 28, No. 1, 1959—Sales less cost		558 0 4
	Biological Flora of the British Isles—Sales		
19	less cost		— — —
	Grants received:		
	Royal Society		1000 0 0
	Net deficit for the year transferred to		
1414	Balance Sheet		— — —
3545			£5208 3 2

1958	*Expenditure*	£ s. d.	£ s. d.
	Working Expenses:		
105	Meeting Expenses	52 14 1	
61	Clerical Assistance	91 1 5	
18	Audit Fee	21 0 0	
5	Addressograph	7 1 9	
1	Bank Charges	14 6	
—	Telephone	5 2 9	
28	Postage	33 19 5	
30	Printing and Stationery	27 12 6	
23	Travelling	47 19 0	
272			287 5 5
	Grants and Subscriptions:		
	British Committee for Nature Conservation	10 0 0	
10	Freshwater Biological Association ...	2 0 0	
	Burren Research Fund	— — —	
25	Council for Nature	— — —	
2			12 0 0
37			
	Journal of Ecology:		
2414	Volume 47, 1959—Cost *less* Sales ...		1075 0 9
	Journal of Animal Ecology:		
229	Volume 27, No. 2, 1959—Cost *less* Sales		478 14 7
	Biological Flora of British Isles:		
—	Cost *less* Sales		7 10 2
	Net Surplus for the year transferred to		
—	*Balance Sheet*		3347 12 3
593	Loss on Sale of Investments		— — —
3545			£5208 3 2

JOURNAL ACCOUNTS FOR THE YEAR ENDED 31 DECEMBER 1959

Journal of Ecology:

Sales:

3537	Current Volume 47		3611 5 5	
519	Back Volumes		1129 11 7	
2414	*Loss on Journal transferred to Revenue Account*		1057 10 6	
	(*Note:* The Stock of Volumes of the *Journal of Ecology* was valued by the Publishers at 31 December 1959 at £14,745)			
6470			£5798 7 6	

Journal of Ecology:

Costs:

	Printing, Paper, Blocks and Binding:		
5118	Volume 47		4387 7 5
26	Binding Back Issues		123 3 0
872	Publisher's Commission		986 17 6
452	Carriage		296 5 7
2	Miscellaneous Expenses		4 14 0
6470			£5798 7 6

Journal of Animal Ecology:

Sales:

1141	Volume 27, Part 2	1140 14 7		
229	*Loss on Journal transferred to Revenue Account*	438 14 7		
			1579 9 2	
—	Volume 28, No. 1	1099 10 11		
1239	Back Volumes	1020 1 6		
4	Abstracts	2 14 5		
1	Notice of Publications			
			2122 6 10	
	(*Note:* The Stock of Volumes of the *Journal of Animal Ecology* was valued by the Publishers at 31 December 1959 at £15,650)			
2614			£3701 16 0	

Journal of Animal Ecology:

Costs:

	Printing, Paper, Blocks and Binding:			
990	Volume 27, Part 2	1315 11 6		
426	Publisher's Commission	209 11 5		
92	Carriage	54 6 3		
787	Reprinting Vols. 12 & 16	— — —		
319	Binding Back Issues	— — —		
			1579 9 2	
	Printing, Paper, Blocks and Binding:			
—	Volume 28, No. 1	1041 10 2		
—	Publisher's Commission	436 1 5		
—	Carriage	86 14 11		
	Profit on Journal transferred to Revenue Account	558 0 4		
			2122 6 10	
2614			£3701 16 0	

BALANCE SHEET AS AT 31 DECEMBER 1959

	Assets	£	s.	d.	£	s.	d.
	Cash at Bank:						
	Westminster Bank Ltd.:						
795	Current Account	1197	3	1			
600	Deposit Account	609	6	5			
1395					1806	9	6
110	*Post Office Savings Bank Account* ...				113	1	8
26	*Income Tax recoverable from Inland Revenue*				23	5	0
	Publishing Account due from Publishers						
	Journal of Ecology:						
	W. Johnson Inc. Sale of Back Issues	1174	2	8			
22	Index Volume	33	8	1			
19	Biological Flora	11	15	2			
		1219	5	11			
	Journal of Animal Ecology:						
	Volume 28, No. 1	558	0	4			
					1777	6	3
	Investments at Cost:						
700	£700 3% Savings Bonds	700	0	0			
1519	£1500 Federation of Rhodesia and Nyasaland 4% Stock 1972/74 ...	1519	3	0			
					2219	3	0
	Loan—Symposium Account				50	0	0
6	*Sundry Debtors*				5	14	8
	(*Note:* The Total Stock of Volumes of the *Journal of Ecology* and of *Animal Ecology* was valued by the Publishers at £30,395)						
3797					£5995	0	1

	Liabilities	£	s.	d.	£	s.	d.
	Members' Subscriptions:						
33	Paid in Advance for 1960 onwards ...				16	3	0
1	*Library Fund*				1	5	0
501	*Burren Fund*				744	4	6
	Publishing Account owing to Blackwells Scientific Publications Ltd.						
30	*Journal of Animal Ecology*				—	—	—
2414	*Journal of Ecology*—Volume 47 ...				1057	10	6
	Reserve of Subscriptions for 1959 (Allocated to second part of *Journal*						
406	*of Animal Ecology*)				416	0	0
	General Revenue Account						
1825	Surplus in hand at 31 December 1958	412	4	10			
	Add: Net Surplus for the year ended						
—*1413*	31 December 1959	3347	12	3			
					3759	17	1
3797					£5995	0	1

I have examined the above Balance Sheet and annexed Income and Expenditure Accounts of the British Ecological Society as at 31 December 1959. I have obtained all the information and explanations I have required, and have verified the Investments and Balance at Bank. In my opinion the above Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Society's affairs, according to the best of my information and the explanations given me, and as shown by the books of the Society.

DEITON COOPER & CO.
124-126 High Street, Edgware, Middlesex. *2 March 1960*

BRITISH ECOLOGICAL SOCIETY

SPRING MEETING AT READING

31 March-2 April 1959

This meeting was held in the Department of Zoology, by kind invitation of Professor Alastair Graham, and was devoted to Freshwater Ecology. The meeting opened on the evening of the 31st with a soirée in the Department, where a number of exhibits illustrating a range of research activities were on display. In the absence of the President, Mr F. T. K. Pentelow took the chair at the meeting the next morning, which was opened by the formal presentation and acceptance of the Society's audited accounts for 1958.

Dr H. B. N. Hynes then read his paper 'On the invertebrate fauna of a mountain stream'. Samples were collected monthly from six stations on a Welsh stream between 235 m and 440 m altitude. Trends in the fauna in the lower four can be partly explained by food supply, flooding and interspecific competition. Seasonally, the species succeed one another so that the important niches are continuously occupied; there is an autumn minimum of larger animals but several small species have summer maxima. Most of the fauna are insects, and though these all hatch from eggs over a long period, they show three main types of life history. In one type hatching begins soon after the eggs are laid but there may be one or two annual generations; in the second hatching is delayed, while the third shows no definite cycle. These life-history types are interwoven to produce the annual cycle and to make maximum use of the available food supply.

Mrs P. A. Horton presented an account of her observations on 'The relationship between the food supply and the requirements of brown trout in acid streams'. Estimates of stream-bottom fauna revealed a large discrepancy between the amount of food available and the annual consumption by the fish. The fauna sampled was that present under stones, while that available to the fish was the excess population ousted from these protecting stones. The delayed hatching amongst some species would also continually add young individuals and enhance the difficulties of accurate population assessment. Sampling of drifting fauna over a shorter period indicated that this might be adequate to satisfy the demands of the trout present, and corresponded to the feeding habits and food of the trout.

After an interval for coffee, Dr K. H. Mann gave a paper on 'The distribution and abundance of leeches'. Quantitative collections in a wide variety of habitats had yielded data on distribution and abundance and these data were discussed with particular reference to the two species of *Erpobdella*. *E. octoculata* is present in all types of running water, and in soft, intermediate and hard standing waters, while *E. testacea* was never found in soft waters and much less commonly than *E. octoculata* in other types of habitat. *E. testacea* particularly favoured shallow reed swamps where the oxygen concentration may reach low levels, and physiological studies showed that it can thrive in lower oxygen concentrations than *E. octoculata*. Except in poorly oxygenated waters, *E. octoculata* is the successful competitor of the two species. In some intermediate conditions *Helobdella stagnalis* may be the most abundant species, and *Dina lineata* dominates in ponds that dry out.

The final paper of the morning was given by Dr T. B. Reynoldson and entitled 'The ecology of lake-dwelling triclads'. The distribution of triclads in lakes shows four patterns related to productivity. These are probably explained by competition for food rather than by the direct action of any physico-chemical factors. Detailed quantitative studies of the life cycles show the disappearance of adults, shrinkage and the accumulation of most of the population in the lower size groups following breeding. After breeding there is a low cocoon production and therefore probably an acute shortage of food which is ultimately relieved by mortality, growth and the reappearance of adults. These life-cycle data suggest that *Dugesia lugubris* would be handicapped relative to *Polycelis* spp. in less productive colder lakes, and in the poorest lakes *P. nigra* can utilize the meagre food supply more efficiently than *P. hepta* or *P. tenuis*.

The afternoon session was opened by a paper entitled 'Notes on river plankton', by Dr J. Rzóska. Both the White and Blue Nile and the joint river carry seasonally, and over long stretches of their course, a true plankton association, showing such typical plankton phenomena as pelagic species, free reproduction, seasonal fluctuations, and 'swarms'. River plankton will develop if there is enough time; the flow of the Nile takes at least 60 days to reach its goal. In the tropics too, the temperature is sufficient for plankton crustacea to develop very rapidly. As each unit of river water has a limited existence there must be a constant renewal of plankton by an inoculum from water bodies where plankton organisms live and multiply in more static conditions.

Dr J. F. Talling followed with a paper on 'The upper limits and limiting factors of photosynthetic production by phytoplankton'. Estimates of photosynthetic productivity when computed per unit area of water surface depend upon the depth of the photic layer and the rate of photosynthesis at various depths within that layer. Examples of the depth distribution of photosynthesis generally show an inverse relationship between these two contributions, with the highest areal productivities developed from intense local rates restricted to a shallow photic layer. Maximal productivity is reached when the algal population itself is the chief cause of the light extinction. Calculations of ceiling values for areal productivity based on data for *Asterionella formosa* in Windermere show that these values are much greater than those actually achieved, which are limited by other, nutrient, factors.

This paper was followed by one on 'Primary productivity studies on a chalk stream', by Mr R. W. Edwards. Techniques for studying the macrophytic vegetation of a stream were described, using quantitative sampling and vertical photography. Estimates were given of the crops produced and the activity of the vegetation in terms of re-oxygenation of streams (*J. Ecol.*, **48** (1960), 151-66).

A third paper on freshwater botany was given by Dr G. A. Prowse, and entitled 'Changes in the vegetation of artificial ponds'. The recent construction of thirty-six ponds in a Latin square at the fish-cultural research station at Malacca allowed observations to be made of the effect on the existing shallow-water vegetation of flooding, liming, fertilizing, cutting and draining and refilling. The emergents *Fimbristylis acuminata*, *Scleria poaeformis*, *Rhynchospora aurea* and *Isachne globosa* could only really be controlled by repeated cutting. Liming encouraged *Chara flexilis*, but this was later replaced after fertilization by *Utricularia* and then *Enhydrias*. A phytoplankton developed with the disappearance of emergents and its components changed with the various manurial treatments.

For the last two papers a return was made to aquatic insects, and Mr N. C. Morgan described the 'Diurnal emergence of aquatic insects' from a small loch near Pitlochry. Apart from the evening emergence of *Caenis horaria*, the *Ephemeroptera* emerged during the day; *Enallagma cyathigerum* emerged between 0800 and 1400 hours; the Trichoptera emerged chiefly after dusk; and *Chaoborus flavicans*, between midnight and dawn. Apart from a few that had a fairly constant emergence rate throughout the 24 hours, the Chironomidae showed two peak times of emergence, midday and after sunset. The time of emergence of the late evening species was related to the rapid change of light intensity at sunset. The midday emergence of spring Chironomids may be of survival value due to low night temperatures.

Finally Mr D. T. Crisp read a paper on 'Estimation of the abundance and mortality of *Corixa germari* (Fiels) (Hemiptera-Heteroptera)'. Quantitative methods of sampling adults and nymphs by pond nets and the counting of eggs attached to stones were described. In 1958 the number of breeding adults averaged 10 per standard net sweep, and these adults produced 916 eggs. Of these eggs about 531 hatched and 80 nymphs survived to the autumn. The 10 adults died in the summer and about 70 of the nymphs died or dispersed over winter leaving 10 adults the next spring.

About seventy members and guests were present at the meeting and nearly every paper was followed by a lively discussion, in which altogether about a quarter of the audience took an active part. Comparison with a similar meeting held in 1952 shows that the trend of interest and research in freshwater invertebrate animals has changed from one concentrating on distribution and species occurrence in relation to physico-

chemical habitat factors, towards a more realistically quantitative approach dealing more intensively with one or a few species, and involving laboratory and field experimentation as well as observation. Information on the population dynamics of the life cycles is now beginning to be available and to be applied to distributional problems.

On the evening of 1 April an informal dinner was held in Whiteknights Park House when members were able to enjoy social contact and informal discussion. On 2 April about twenty members were taken on a tour of freshwater habitats near Reading under the guidance of Dr Mann. First we went to the University of Reading's laboratory on the River Thames where demonstrations of the research in progress and specimens of the local fish and invertebrate fauna were on display. Then the headwaters of the River Pang were visited and finally a pond and runnels on clay and plateau gravel.

We are grateful to Professor Graham, other members of the Zoology Department at Reading, the Warden of Whiteknights Park House and especially to Dr Mann for a most successful and stimulating meeting which demonstrated that freshwater ecologists are among the most active members of the Society, and that Reading was an excellent place to choose for a meeting devoted to freshwater ecology.

E. D. Le Cren

THE BIOLOGY OF WEEDS

First symposium meeting organized by the British Ecological Society, Oxford, 2-4 April 1959

The majority of the papers presented at this first symposium will be published in mid-1960, and therefore this record is brief. The meetings were held in the Clarendon Laboratory, Oxford, and accommodation was provided in Brasenose College.

Thursday, 2 April

On behalf of the President, Dr J. L. Harper (Oxford) welcomed non-members to the symposium.

Dr H. Godwin (Cambridge) presented the opening paper, 'The origin of the weed flora of Britain'. Professor A. H. Bunting (Reading) reflected on the ecology of weeds, and Dr H. Leith (Stuttgart-Hohenheim) presented some interesting data on the movement of plants in both natural and artificial grassland communities.

The afternoon session was devoted to a consideration of the taxonomy and evolution of weeds. Dr E. F. Warburg (Oxford) outlined several taxonomic problems which existed in weed species, and he was followed by speakers who dealt in detail with some of these problems. Mr B. T. Styles (Oxford) spoke on 'Taxonomic problems in *Polygonum aviculare*', and Mr A. Pettet (Southampton) on 'Some problems in *Viola tricolor* and its allies'. Dr T. O. Pritchard (Nature Conservancy) discussed race formation in weed species and drew his main examples from *Hypericum perforatum* and *Euphorbia cyparissias*.

On Thursday evening many gathered at West Wood House to enjoy the hospitality so kindly offered by Professor and Mrs Blackman.

Friday, 3 April

The morning meeting was concerned with the dormancy and dispersal of weed seeds. Miss J. M. Thurston (Rothamsted) reviewed the complex subject of dormancy and Dr N. Sunderland (Bayfordbury) discussed the special germination characteristics of some angiospermous parasites. Dr P. S. Wellington (National Institute of Agricultural Botany) demonstrated the usefulness of official statistics when they are properly used. He spoke on the 'Assessment and control of the dissemination of weeds by crop seeds', and drew his information from records collected by the National Institute of Agricultural Botany over the years. Miss S. Hitchings (N.I.A.B.) followed Dr Wellington and considered the ways by which weeds could be controlled and eliminated from seed crops as a result of a knowledge of the biology of those weeds.

The afternoon session was entitled 'Population Studies, Interference and Competition'.

Dr J. L. Harper (Oxford), Mr J. N. Clatworthy (Oxford) and Dr J. K. A. Bleasdale (National Vegetable Research Station) outlined their respective views on the ways in which plants interfere with each other and the results of such interference. After tea, Dr P. Martin (Stuttgart-Hohenheim), Professor Dr G. Grümmer (Griefswald) and Dr P. J. Welbank (Rothamsted) presented evidence on the hypothesis that plants can affect the growth of other plants by the production of toxic substances. A little after 6 o'clock the afternoon session ended and there was a necessary breathing space until 8.15 p.m. when Professor A. H. Bunting (Reading), the chairman of this session, began a summing up of the six papers. Whatever the inner feelings of the chairman, his choice of words was sufficient to provoke both big fish and little fish to verbal warfare. The discussion did ultimately end just before the doors of Brasenose College were finally closed for the night. It is impossible to summarize, in a short space, the views expressed, but it is sufficient indication to say that if ninety-two persons attended the discussion, then there are at least ninety-two different meanings for the word 'competition'. More seriously, however, it must be placed on record that many of those who came to this discussion expressed the feeling that they had never before experienced a more exhilarating evening organized by a learned society.

Saturday, 4 April

The morning was devoted to 'Special Weed Problems'. Dr E. K. Woodford (Oxford) spoke on the general problem of woody weeds and Dr G. W. Ivens (Oxford) and Dr E. C. S. Little (Oxford) followed with brief contributions on selected species. Mr J. D. Fryer (Oxford) outlined the difficulties caused by water weeds and Dr P. A. Gay (Nature Conservancy) spoke from personal knowledge of the recent invasion of the Nile by *Eichornia crassipes*.

The only departure from the advertised programme occurred at this point (one of the speakers being unable to attend) and the conference received a paper by Dr A. S. Watt (Cambridge) who described his long-term experiments on the fluctuations in population size of various species in permanent quadrats in Breckland. Dr K. Holly (Oxford) briefly described the major problems associated with parasitic weeds and Mr W. G. Weeraratna (Oxford) summarized his investigations into some economically important species of the parasitic Loranthaceae.

It was unfortunate that many of those attending had to leave at lunchtime in order to return home, but for those who did remain the contribution by Dr D. Bakker (Ens, Holland) was amply rewarding. Dr Bakker, by approaching an applied problem from a fundamental viewpoint was able to gain an understanding of the two most troublesome weeds in newly reclaimed polders of the former Zuider Zee, *Cirsium arvense* and *Tussilago farfara*. Dr A. Lazenby (Cambridge) described his experiments on weed species of *Allium*. Mr G. R. Sagar (Oxford) and Mr M. J. Chadwick (Bangor) ended the session by describing some of their ecological work on *Plantago* spp. and *Nardus stricta* respectively.

Professor A. H. Bunting, speaking on behalf of everybody who attended the conference, expressed thanks to Professor Bleaney for the facilities extended by the Clarendon Laboratory, to Professor Blackman for the help given by the Department of Agriculture, and to the staff of Brasenose College who housed and fed the conference so well.

The symposium Committee consisted of Dr J. L. Harper, Dr E. K. Woodford and Mr G. R. Sagar.

G. R. Sagar

SUMMER MEETING AT GALWAY

3-8 September 1959

Some forty members of the Society assembled for the 1959 Summer Meeting, held at Galway from 3 to 8 September, and based on the Golf Links Hotel at Salthill. On the evening of 3 September, Professor D. A. Webb gave an introductory talk on the region at University College, Galway. He stressed the interaction of the Atlantic climate of western

Ireland and the geology, dominated to the south of Galway by Carboniferous limestone, on the impoverished fauna and flora. This impoverishment is due partly to lack of suitable ecological habitats and partly to the early isolation of Ireland in Post-glacial times. One striking effect of the Atlantic climate, of the reduced flora and of other factors is the curious mixture of supposed 'calcicoles' and 'calcifuges' which occur in some habitats. Professor Webb's talk was followed by refreshments for which we are most indebted to our Galwegian hosts.

On Friday, 4 September, the party set out in a convoy of cars and visited first two small areas of saltmarsh near Oranmore. The first appeared to be fairly heavily grazed but had a varied flora and an interesting drainage system. The second was notable mainly for the abundance of *Artemisia maritima* (uncommon in Ireland) at the higher levels.

The shores of Lough Derg were visited near Cregg Point. After lunch, members were able to compare the lush reedswamp vegetation of the muddy shores (*Phragmites communis, Glyceria maxima, Scirpus lacustris*) with the more barren stony shores. Mr Yapp saw two woodwarblers which are unusual in this part of the country.

The day finished with a visit to a raised bog east of Woodford. Marginal peat cuttings were examined, and Mr Watts expounded on the profile seen. The most obvious change, from the upper light-coloured fresh *Sphagnum* peat to a lower darker peat occurred at a depth of 45-60 cm and was thought to be referable to a date between A.D. 200-300. On the bog surface Dr Proctor demonstrated several species of *Sphagnum* including *S. imbricatum, S. fuscum*, and a fine growth of *S. pulchrum*. The discussion of regeneration complexes was suitably inconclusive. The centre of this bog aroused curiosity and scepticism. It had formerly contained an open pool which was now completely colonized, and the site surrounded by a copse of flourishing *Betula pubescens*, with well-grown *Myrica gale* and luxuriant *Vaccinium oxycoccus*.

On the next morning the car convoy travelled through the southern part of Iarconnaught, characterized by small stony fields with shallow soils. Near Costelloe the party saw the proliferating unattached form of *Ascophyllum nodosum*, forma *mackaii*, and some very dwarf saltmarsh fucoids. A longer stop was made near Carraroe, where the main features were the 'coral' beaches almost entirely composed of dead *Lithothamnion calcareum*, the rock pools which contained an abundance of the spiny sea urchin, *Paracentrotus lividus*, and a remarkably rich algal flora, expertly demonstrated by Dr De Valera. The low tide revealed the complete zonation from *Lichina pygmaea* and *Pelvetia canaliculata* at the top down to the *Laminaria* zone.

After lunch on the beach we went to an area of blanket bog near Screeb. This appeared to be so obviously subject to flushing as to give rise to considerable discussion about the true nature of blanket bog. The area examined appeared to have more lush *Schoenus nigricans* and *Molinia coerulea*, and less *Sphagnum*, than other less flushed areas. A deep slow stream flowing through the area contained, among other species, *Eriocaulon septangulare* and *Lobelia dortmanna*. A brief stop was then made near Maam Cross to see *Cladium mariscus* and *Eriocaulon* in a small lough, and also *Daboecia cantabrica*.

The final item on the day's agenda was the ascent of Lissoughter (1314 ft) near Recess, in a stiffening breeze. The flora was varied and included *Saxifraga oppositifolia, S. spathularis, Dryas octopetala, Asplenium viride, Selaginella selaginoides* and *Lycopodium selago*. The weather held fine, and moderate visibility allowed an interesting view of the Twelve Bens, and of Connemara scenery as a whole.

The first stop on Sunday, 6 September, was at Cloghmoyne, a low limestone hill near Headford. We examined a calcareous heath, a mixture of supposedly calcicole and calcifuge species growing together. These included:

Calluna vulgaris
Erica cinerea
Potentilla erecta
Pteridium aquilinum
Agrostis tenuis
Dicranum scoparium
Galium verum
Sieglingia decumbens
Campanula rotundifolia
Geranium sanguineum
Briza media
Carlina vulgaris
Blackstonia perfoliata
Sesleria caerulea
Plantago maritima

The limestone pavement near the top of the hill provided *Thelypteris robertiana* (in its

only Irish station), *Vicia orobus* and *Rubia peregrina*. Heavily grazed shrubs of hazel, ash, rowan, holly, willow, blackthorn, hawthorn and spindle poked out from the limestone grykes. There was much discussion as to the origin of limestone pavement. Pebbles and boulders of sandstone suggested a former drift covering, and there is some geological evidence that the sculptured weathering of the limestone to form a pavement could only have occurred under a drift covering. On the other hand if there was a drift covering, where has it all gone? The gentle undulating topography of the limestone was maintained all around; the drift had not been washed down to fill up the hollows below. The floristic evidence was conflicting; some species at present growing there might require an open habitat, such as *Vicia orobus*, but others, such as *Anemone nemorosa* might be woodland relicts. No conclusion was reached.

At the second stop, Keel Bridge, luncheon was taken in slightly 'soft' weather, and an examination made of limestone pavement between Loughs Mask and Carra. The free regeneration of pine in this pavement was noted. Juniper was quite abundant but very prostrate. On the other side of the road, protected from grazing, it was growing 10 ft high. Lough Carra itself contains a calcareous marl, with remnants of *Chara* in it, and the highly calcareous conditions in the lake itself seem inhibitory to fauna and flora. The marginal *Schoenus* fens are floristically rich; Professor Clapham found a still recognizable specimen of *Dactylorchis cruenta*, though most of the orchids for which this area is famous were not identifiable so late in the year.

The west shore of Lough Mask, which was visited near Gortmore, was a complete contrast, for here the shore is sandstone, though the lake water is highly calcareous. Professor Webb demonstrated *Hypericum canadense*, a North American species which he had recently discovered in Ireland. It was growing in an iron-rich flush, with *Sphagnum subsecundum* and *Hypericum elodes*. Also present were *Lycopodium inundatum* and *Pilularia globulifera*. The flush passed through a grassy sward which showed a gradual transition from an acidic grassland (with *Nardus stricta*) at the landward side to a mixture of sand colonizers (*Salix repens, Potentilla anserina*) and hydrophytes (*Apium inundatum, Hydrocotyle vulgaris, Callitriche* sp., *Myriophyllum* sp.) at the lakeward side. The whole area was greatly influenced by the grazing of cattle, sheep and geese.

A brief stop was made half a mile further on to look at an impressive array of pine stumps of presumed late Boreal or Atlantic age. They had been laid bare over a large area by peat cutting or erosion. Professor Webb invited us to picture Ireland with large areas of pine forest, with a hazel understorey, as suggested by pollen analysis.

We had tea at Ashford Castle near Cong, a massive monument to Guinness in the Balmoral style, now run as an hotel in a beautiful site on the shores of Lough Corrib.

The following day was warm and sunny, and the diminishing party visited the western part of the Burren. A brief halt was made between Lisdoonvarna and the top of the Corkscrew Hill where Professor Webb demonstrated the transition from coal measure shales to Carboniferous limestone. The shales give a tenacious clay soil, which allows growth of *Juncus effusus* on quite steep slopes.

The next stop was north of Poulsallagh where there was a grassy sward at the top of 100 ft limestone cliffs. Above the road were further areas of limestone pavement. The flora was a mixture of maritime species (*Aster tripolium, Armeria maritima, Plantago maritima, Crithmum maritimum, Limonium binervosum*, probably the form called *L. transwallianum*) and limestone species (*Minuartia verna, Carlina vulgaris, Geranium sanguineum* and *Sesleria caerulea*). *Calluna* appeared to be growing with some roots in direct contact with limestone.

After moving on to Fanore Bridge the party examined sand dunes there, and also the small Caher river, the only river in the Burren district. Mr Le Cren found that this stream contained trout and eels, and a fairly extensive permanent stream fauna. There is hardly any new dune formation due to lack of sand, but the existing dunes showed a number of blow-outs and stages of colonization. The sand was very calcareous so that there was no tendency for the dune vegetation to progress to a heathy stage. *Euphorbia paralias* was very abundant, and Professor Clapham distinguished the less common but rather similar *E. portlandica*. There was a great extent of *Ammophila arenaria* which did not appear to flower in this locality. The seashore itself had a fairly rich fauna and

flora for so exposed a site, including several attractive rock pools. *Paracentrotus lividus* inhabited small, neatly fitting depressions in the rock whose origin gave rise to speculation. *Mytilus edulis*, very small in size, was extremely abundant. Among the seaweeds, *Bifurcaria tuberculata* and *Codium tomentosum* were both abundant. There were few sponges or tunicates. As we returned to the cars, a pair of choughs attracted a large audience.

The final event of the day was the ascent of Carnsefin (1045 ft), near Black Head, an exposed limestone headland mainly composed of flat steps of limestone pavement, with small, near-vertical 'cliffs' between. There was a zonation, with *Sesleria* grassland on the lower slopes, followed altitudinally by a zone in which *Dryas octopetala*, *Asperula cynanchica* and *Calluna* were abundant. *Dryas* persisted to the top, associated in successive altitudinal zones with *Empetrum nigrum*, *Arctostaphylos uva-ursi* and near the summit *Rhacomitrium lanuginosum*. The great luxuriance of *Dryas* was impressive. A few patches of *Saxifraga rosacea* were seen near the road, *Epipactis atrorubens* was frequent during the ascent and a single (bird-sown?) plant of *Cotoneaster microphylla* adorned the summit cairn.

In the evening, an informal discussion about the Burren was held at the Golf Links Hotel. Professor Webb posed the main problems, but even his enthusiasm stimulated few tangible offers of assistance. The central problem of the Burren is the great extent of bare limestone which gives it its name. Was this drift-covered at the end of the last glaciation? Dr R. J. Jones thought this likely, that the drift had gradually slipped down the grykes and the calcifuge drift flora was being replaced by a calcicole limestone flora. The presence or absence of the little pits on the surface of the limestone left by the apothecia of endolithic lichens could be used to indicate whether an area of rock had recently been bare or not. Mr Watts stressed the need for archaeological evidence. It seemed that the logical sequence would be to study first the glaciology and recent geological history of the region, next the soils and finally various autecological problems including the distribution of *Corylus*, *Dryas* and *Calluna*. Professor Burges took this opportunity of extending thanks, on behalf of the Society, to Professor Webb and Mr Watts for the excellent organization of the meeting, and to Dr De Valera, Mr Mitchell and their colleagues from the University College of Galway for much local assistance.

On the final day, a much reduced party visited the eastern part of the Burren, between Gort and Corofin. The first stop was to look at a turlough at Tirneevin. The very dry summer had left no open water, though the mud was still moist. *Cinclidotus fontinaloides* and *Fontinalis antipyretica* were both abundant on the rocks and stone walls which are submerged in the winter. The line of the hawthorn scrub indicated the highest water levels. There was a curious intermingling of terrestrial and aquatic plants, including small, rooting, terrestrial forms of *Potamogeton natans* and *Myriophyllum* sp. A few live aquatic snails, including *Limnaea pereger*, were found under moist moss.

The ruined monastery of Kilmacduagh was then expertly demonstrated by Professor Duignan, Professor of Archaeology at Galway. The legend of its founding referred to St Colman, the founder, as walking through 'a dense forest'. The authenticity of the legend is presumably open to doubt but its ecological importance was appreciated. The monastery was a group of small scattered churches with a very fine example of a round tower, used for defence, and isolated from, but near to, the principal church.

Lunch was taken near Lough Bunny, one of the largest of the permanent lakes on the Burren. It is very shallow, and the water is highly calcareous, the shores and the lake bottom having a heavy calcareous deposit. There was no littoral fauna or flora. The marl exposed by the low level of the water was interrupted by large patches of peat; it was impossible in the limited time to decide whether this was redistributed or was fen, flooded by a rise in water level. Another turlough was examined near Aglish. It was fringed by some fine bushes of *Potentilla fruticosa*, and also contained *Teucrium scordium* and a linear-leaved form of *Baldellia ranunculoides*, which most of the party mistook for *Littorella uniflora*.

Finally the party examined ash-hazel woodland on the limestone hill of Mullagh More (627 ft), which carries one of the best areas of woodland remaining in the Burren, possibly representative of much of the Burren before the iron-smelters came. Before entering

the woodland, some holes were dug in an area where rather impure limestone had weathered to produce a soil covering thicker than is usual, with about 6 in. of raw humus overlying the mineral soil. The woodland itself had a fairly open canopy with hazel rising to 12-15 ft in the centre of the wood, and ash to at least 40 ft. Associated trees included *Crataegus monogyna, Betula pubescens, Ilex aquifolium, Salix caprea, Sorbus aucuparia* and *Ulmus glabra.* Goats and cows were numerous in the wood, and seedlings correspondingly rare, though some of ash and elm were seen. The ground flora included *Holcus mollis, Oxalis acetosella* and *Hedera helix* in abundance.

Tea at Gort provided a fitting conclusion to this meeting, which was blessed throughout with unusually fine weather.

P. J. Newbould

WINTER AND ANNUAL GENERAL MEETING

8 and 9 January 1960

Professor D. Lewis welcomed over a hundred members at the start of the Winter Meeting, 1960, in the Department of Botany, University College, London. Three papers were read during the afternoon of Friday, 8 January. In the first, concerned with 'The ecology of the St Kilda field-mouse', Dr J. Morton Boyd said that the St Kilda mice were first noticed by scientists in 1878 and both species, a house-mouse and a field-mouse, were described by the end of the century and were given the names *Mus musculus muralis* and *Apodemus sylvaticus hirtensis* by Barrett-Hamilton. In 1930 St Kilda was evacuated and it is thought that the house-mouse became extinct after 2 years. The field-mouse on the other hand was released from the predation of the domestic cats and dogs. There are now no predators of the mouse except the raven and large gulls. In 1955, 100 trap-nights achieved the same catch as 650 trap-nights using the same method in 1931, and in 1956-59 the population remained consistently large by comparison with 1931. In 1956-57 a radar station together with camp and roads were built on the island of Hirta; about 300 men were stationed there in summer and 40 in winter. This upheaval did not appear to affect the field-mouse population significantly. A survey in 1957 showed that mice were widespread in and around stoneworks (natural and artificial) in all the main ecological zones; they were most numerous in the derelict village and scarcest on the summits and ridges. Arising from a certain amount of nuisance caused by mice in the camp, investigations were made into the movements of the animals with an eye to transplanting the community in the village area to other parts of the island. Trap surveys showed that animals could range over $\frac{3}{4}$ acre in the village in a few nights and that if removed up to $\frac{1}{2}$ a mile from the village area would return to the site at which they were trapped, in some cases within a few hours.

The breeding season is similar to mainland populations and is determined by the females: conception is probably in late April, the young appearing in the traps in late June. Parasites include three fleas and two mites. There are heavy infestations of the nematode *Rictularia cristata* and the cestode *Hymenolepis diminuta. Cysticercus fasciolaris,* the larva of *Taenia crassicolis* (the cat tape-worm), found in 1931, has not been found in recent dissections and is probably extinct at St Kilda.

Professor N. A. Burges, Dr E. W. Bentley, Mr I. J. Linn, Mr R. A. Davis, Mr M. J. Delaney, Dr G. M. Dunnet, and Mr P. A. Jewell took part in subsequent discussion, in which the importance of the shelter provided by cleats and other stoneworks was emphasized.

Dr P. J. Newbould, speaking on 'The ecology of Hartland Bog and Fen, Dorset', commented that recent work, especially in Scandinavia, has demonstrated correlations between the chemical analysis of mire waters and vegetation. Water movement, which is difficult to measure, is probably also important in this connection.

Dr Newbould, referring to lantern slides, showed that on Hartland Moor, in Dorset, two converging arms have differing vegetation. The northern, or valley bog, arm has a continuous carpet of *Sphagnum* with occasional plants of *Schoenus nigricans*, whereas in the southern, or fen, arm there is only a narrow zone of *Sphagnum* lateral to the main area of water flow which is dominated by dense tussocky *Schoenus* with abundant

Campylium stellatum. The vegetation below the point where the two arms join is intermediate. There is a reasonable correlation between the distribution of vegetation types and the pH and calcium content of the water. The source of the calcium-rich water of the fen arm may be the chalk foundation of the main road.

Estimates of the (mainly annual) standing crop of three sites were similarly correlated with water analyses, the productivity of the fen being apparently greater than that of the valley bog. The ash and base contents of the plant material were determined. These two sets of data were combined to give an estimate of base turnover in the three sites. Calcium, expressed either as turnover per unit area, or as a percentage of the dry weight of the standing crop, is considerably higher in the fen than the valley bog. Differences in sodium and potassium are smaller. A comparison of these figures with the water analyses showed that potassium is concentrated by the vegetation much more than calcium or sodium. It seems unlikely that calcium supply has a *direct* limiting effect on the vegetation. The differences in base turnover can be explained by differences in water analysis in the three sample areas, without invoking differences in water movement, though the latter must occur.

Finally the density, height growth, dry weight per unit area and tussockiness of *Schoenus nigricans* on Hartland Moor are closely related to the base status of its environment.

The possibility of estimating the rate of supply and replacement of water was discussed by Professor J. B. Cragg, Dr E. B. Worthington, Mr H. C. Gilson and Mr R. Clymo; other points were raised by Dr D. S. Ranwell, Dr J. M. Lambert and Mr Bellamy, who mentioned another example of a roadway acting as a source of calcium.

Completing the afternoon's session, Dr J. Phillipson gave an account of 'The feeding biology of *Mitopus morio* (Fabricius) (Phalangida, Arachnida)', which he introduced by pointing out that before a reliable picture can be formed of energy transformations within a community, more information must be available on the efficiency with which animals in nature utilize their food materials. The two most often used indices of metabolic activity are the respiratory rate and the '*Konsumquotient*'. The former is of great value in studying small organisms whereas the latter has been used for more readily handled species. However, both methods have attendant disadvantages as the experimental animal has to be studied in the laboratory under conditions of temperature and humidity that do not always simulate those of the natural environment. In the present work on *M. morio* an attempt was made to eliminate these disadvantages and to obtain a measure of the energy transformation brought about by all the developmental stages under natural conditions.

Examination of faecal pellets, laboratory feeding experiments and field observations showed *M. morio* to be a general predator. Only animals with a thick exoskeleton, much mucus or species much larger than the predator escaped capture.

Knowing the animal's food, laboratory feeding experiments showed that the amount of food assimilated, expressed as a percentage of the weight of food eaten was highest in instar 2 (74%) and fell to 47% in the adult. Food consumption under field conditions ranged from 0·46 cal. per day in instar 2 (average live weight 1 mg) to 2·98 cal. per day in adult males (average live weight 26 mg) and 5·74 cal. per day in 6th instar females (average live weight 17 mg). The corresponding average calorific values for food assimilated per day ranged from 0·34 cal. in instar 2 to 1·39 cal. in adult males and 2·53 cal. in 6th instar females.

The '*Konsumquotient* (KQ), expressed as $c/\sqrt[3]{g^2}$ where c represents food consumption or faeces production and $\sqrt[3]{g^2}$ the surface area of the animal, was not approximately constant and therefore not directly proportional to the surface area of *M. morio*. The 'constant' was affected by the physiological state of the animal and is thus of limited value for the study of metabolic activity.

Answering a variety of questions from Dr S. R. J. Woodell, Dr D. S. Ranwell, Mr E. D. Le Cren, Mr B. Heighton, Dr J. L. Cloudesley-Thompson, Dr J. Morton Boyd, Mr I. J. Linn, Mr J. G. Skellam and Mr G. Williams, Dr Phillipson explained that although the animals may move about in high humidities in the dusk, they are not active hunters; most of their food is taken in the early hours of darkness and capture seems to depend

upon physical contact with the prey. During the day shelter is sought under grass, stones, etc.

In the evening an informal dinner in the pleasant atmosphere of the Upper Refectory, University College, was followed by a soirée in the North Cloister, where numerous exhibits were on view. The Botany Department of University College demonstrated some useful ecological apparatus, and Mr R. Clymo showed an apparatus used in water-culture experiments, as well as an exhibit on the problem of the calcicole type of distribution and its investigation. Mr S. B. Chapman contributed illustrations on Coom Rigg Moss, Northumberland, and Mr I. G. Simmons showed a preliminary map of the blanket peat of Dartmoor. The Freshwater Biological Association had on view a sampler for the superficial deposits of the bottoms of lakes and J. H. Belcher demonstrated pigments of lake-bottom sediments. Exhibits of photographs included a selection from Blakeney Point, Norfolk, by R. Brindsen and a selection of aerial photos by Dr J. K. S. St Joseph. Other botanical exhibits were by Mrs J. P. Newbould, on the distribution of *Dryopteris borreri* Newn. in the British Isles; E. I. Newman on the effects of soil disturbance and soil moisture on *Teesdalia nudicaulis*; Miss B. C. Barratt on some grassland humus forms, mainly from Malham Tarn, Yorkshire; and D. Munro on trenched plot experiments in the New Forest. On the zoological side, Dr D. J. Crisp showed some animals of the east coast of N. America and R. O. Brinkhurst demonstrated wing polymorphism in the British Gerroidea.

On Saturday morning, 9 January, following the Annual General Meeting (see below), Professor P. W. Richards gave a paper on the 'Peat swamps of Borneo'. In Malaysia extensive peat swamps are found at low altitudes, especially in Borneo, Sumatra and New Guinea. They occur mainly near the coast and always in regions of high rainfall with no well-marked dry season. The peat swamps of north-western Borneo have recently been carefully studied by Mr J. A. R. Anderson of the Sarawak Forestry Department and this paper deals partly with his work and partly with Professor Richards's observations during a visit to Brunei and northern Sarawak in March-April 1959.

The peat swamps have a convex surface and are analogous to the raised bogs of temperate climates. The plant communities form more or less concentric zones and are dominated by trees. In some zones the Dipterocarp *Shorea albida* is dominant to the exclusion of almost all other tall-growing species. The zonal communities form a series with respect to number of species (which diminishes towards the centre), abundance of *Nepenthes* and other features.

A boring by Muller and Anderson at Marudi in Sarawak showed that the peat may be as much as 13 m thick and the pollen profile suggests a succession beginning with mangrove and ending with the stunted *Combretocarpus-Dactylocladus* community ('padang paya'). The radiocarbon dating of peat at 12 m is 4040 ± 70 years.

These peat swamps offer a variety of interesting problems for future investigation.

The paper was illustrated by coloured slides and by a collection of aerial and other photographs kindly lent by Mr J. A. R. Anderson. Following it, questions were asked by Dr A. S. Watt, Dr J. M. Lambert, Dr E. W. Jones, and Dr A. E. Apinis. Professor Richards said that bryophytes do not play an important part in the swamp forests, apart from a number of hepatics on the pneumatophores; otherwise epiphytes are not abundant.

In the second paper, on 'A graphical model representing various mechanisms of population control', Mr G. G. Vickers suggested that a synthesis of all current views concerning the modes of population control depends on clear definition of what are at present somewhat confused concepts. The operation of the *population-environment* system is still a controversial matter because semantic difficulties obscure the nature of the components and the interactions involved. Synthetic mathematical treatment of the system cannot succeed until the concepts to be manipulated are clearly definable.

Representation of the *population-environment* system by a physical model may be rewarding, since such a model may be made obedient to many different influences operating simultaneously. Mr Vickers described an earlier attempt to construct a population control model (Proceedings, XV International Congress of Zoology, 1959); this model appears inadequate in that it cannot allow for the fact that mortality is

imposed simultaneously by many different influences. He outlined a new approach to a model: a population is represented as an elastic body contained within a variable pressure chamber representing ambient physico-chemical conditions. Metabolic process within the population is supported by an energy and a material input, and is subject to a variable load representing diversion of energy from the population. The size of the population will vary according to its metabolic output; this is susceptible of alteration at four *control points*, namely 1/Energy input, 2/Material input, 3/External pressure, 4/Load imposed.

Energy flux through the population will be adjusted through natality and mortality, and these will be varied by alteration at one or more of the four control points; the controls may be independently operated, interlinked extrinsically, or linked intrinsically through feed-back mechanisms proportionate to the population.

If concepts of population control mechanisms can thus be translated into physical terms, an actual model might be constructed in collaboration with control-system engineers: such a model would enable the possible interactions of the various control mechanisms to be realized. The forms of these interactions could then be compared with field and laboratory studies of actual populations; in this way a closer approach to a truly general theory of population control mechanisms might be made.

The paper was welcomed as a new way of thinking by Mr J. G. Skellam, who, with Professor J. B. Cragg and Mr G. R. Gradwell, selected particular aspects for critical comment.

The final session in the afternoon was opened by Dr G. M. Dunnet, speaking on 'A study of a population of rat-kangaroos (*Setonix brachyurus*) using the recapture technique'. This paper was an outline of a study of the quokka (*S. brachyurus*) in its semi-natural habitat on Rottnest Island, off Freemantle, Western Australia. The quokka is a small wallaby, comparable in size with the brown hare, and is herbivorous and mainly nocturnal. During the study over 3000 were caught and tagged, and over 5000 captures were recorded. The animals occur all over the island, and on the eastern end, during the hot dry summer months of December-March they congregate at night on a limited number of fresh or brackish water seepages, to drink. Movement of tagged animals in relation to the seepage was described and it was concluded that several remarkably discrete sub-populations of quokkas exist in different areas of the island, those on the western areas not coming to the drinking places at all.

Young quokka remain in the pouch for about 5 months and by measuring them at each capture, growth-rates and birth-dates were calculated. The season of birth extends from late January to early November, but most young are born in February, March and April. Growth and size of different age-groups was described.

The main object was to estimate population size and death-rate using the recapture technique and after several trapping procedures had been tried, the most attractive seemed to be the use of a long net at the drinking places throughout the summer. A sampling programme involving netting at 2-hourly intervals from 9.00 p.m.- 2.00 a.m. on three consecutive nights, once in each monthly period, gave usually between 100 and 200 captures per month. The nature of the sample was considered in detail and thought to be consistent with random sampling in regard to drinking behaviour throughout the night and constancy of place and time of drinking, but young animals in general tended to be caught more readily than old ones and in the estimation these had to be considered as two separate populations. It was also considered that the problem of trap addiction and probably trap-shyness had been eliminated, at least to some extent, in the inter-period analyses.

Despite these apparently favourable circumstances, and with the order of 45-60% of the population marked in each of 3 years, only very approximate estimates were obtained. Not only were these estimates imprecise but their relation to the population may be questioned. Thus, samples from populations of which some individuals are marked can tell us much more about the biology of a species than sampling without marking, but the use of the recapture technique for the estimation of population parameters must always be investigated with special care.

The merits of the recapture technique were discussed by Mr E. D. Le Cren, Dr R. O.

Brinkhurst, Professor O. W. Richards, Mr J. G. Skellam, Dr D. H. Chitty, and Mr H. N. Southern.

The final two papers were both concerned with the ecology of the South Atlantic islands (the Tristan da Cunha-Gough Island group). Mr N. M. Wace spoke on 'Some aspects of plant ecology and phytogeography in the South Atlantic islands'. The Tristan da Cunha-Gough Island archipelago in the South Atlantic is a remote group of oceanic islands, probably formed very recently, and having a warm temperate hyper-oceanic climate. On Gough Island, five vegetational formations can be recognized.

Maritime Tussock Grassland on the sea cliffs and in penguin rookeries, formed by *Poa flabellata*, closely resembling some tussock communities in the New Zealand shelf and southern Indian Ocean islands, and with some similarities to grass steppe. On all the islands in which it occurs this formation is very vulnerable to the effects of grazing animals.

Fern Bush which is dominated by *Phylica arborea*, forming dense thickets amongst the small tree-fern *Blechnum palmiforme*, and *Histiopteris incisa*. Mosaic formation by the different components of this community is dependent upon autogenic cyclical processes involving the rapid build-up and slipping away of peat accumulating on the steep slopes. The formation is structurally related to widespread tropical mountain vegetation types ('mist forest', 'microphyll mossy thicket', 'heath forest', 'elfin woodland'), and is unlike the southern continental *Nothofagus* forests.

Oceanic Heath, forming blanket peat above the Fern Bush and Tussock Grassland communities, dominated by *Empetrum rubrum*, grasses and sedges, with patches of *Sphagnum* and other bryophytes. This community resembles structurally the Magellanic moorland of western Chile, and the wet moorland vegetation of western Europe.

Feldmark in the most exposed areas above 750 m, with isolated tufts of *Agrostis media*, mats of *Empetrum* and *Rhacomitrium*, and hummocks of close-growing bryophytes. This community on Gough Island lacks the cushion-forming flowering plants of higher southern latitudes (*Azorella*, *Colobanthus*).

Bogs of deep (to 4·5 m) *Sphagnum* and Cyperaceae peat, formed in the mountain valleys, resembling structurally the dissected montane valley bogs of north-west Europe. Shallower and less dissected peat deposits formed by Bryales and Hepaticeae cover some of the mountain plateaux. Bogs dominated by cushion-forming flowering plants (*Donatia*, *Astelia*, etc.) as found in New Zealand and South America do not occur in the Gough-Tristan group.

Some of the ecological effects of their insularity and oceanic climate include:

(i) The high proportion of pteridophytes to flowering plants (27/32 species on Gough, cf. 34/about 325 native on Rhum), correlated with the great importance of ferns in the vegetation.

(ii) The extreme species-poverty (0·5 native flowering plants per square km on Gough, cf. 3·0 native fl. plants/sq. km on Rhum) and lack of annuals, together with the lack of species adapted to withstand the conditions created by man (grazing, clearance, fire, etc.), leading to vegetational imbalance and vulnerability to changed conditions or competition from new arrivals.

Owing to these peculiarities, the island formations are not strictly comparable to continental climax formations because the species present on the islands are selected primarily for their capacity to achieve long-distance dispersal. Structural rather than floristic or phytosociological criteria must be used in comparing their vegetation with that of other areas.

Comments on the effects of grazing on the Tussock Grassland were made by Professor J. B. Cragg, Dr E. J. Godley and Dr G. M. Dunnet.

Dr M. W. Holdgate, in the last paper, considered some 'Aspects of animal ecology in the South Atlantic islands'.

The Tristan da Cunha-Gough Island group has an impoverished and disharmonic terrestrial fauna. One hundred and thirty-two species have been recorded and of these forty-five are probably alien: about 65% of the native species are believed endemic. The fauna shows strong South American relationships and is thought to have invaded

the islands comparatively recently largely by airborne immigration in the prevailing westerly winds.

A study of selected habitats emphasizes the poverty of the fauna. On Gough Island only eight species have been recorded in fresh water, and two of these are known elsewhere only from marine habitats. Three of the remaining six are carnivorous, and a Dytiscid beetle (*Lancetes varius* F. *dacunhae* Brinck) ranges most widely of all. Various features suggest a low level of interspecific competition and probable underexploitation of the habitat. These features are also apparent in terrestrial situations. Many of the common plants are attacked only by one or two phytophagous species: for example one Lathridiid beetle (*Coninomus* sp.) is alone abundant on the fern *Histiopteris incisa*, a Delphacid (*Delphacodes atlanticus* China) and a weevil, *Tristanodes* sp., are associated with *Scirpus* spp. and two or three aphids with *Apium australe*. Some niches seem to be unfilled, there being for example no specialized wood-boring insect larvae which attack the dominant tree *Phylica arborea*. Yet despite this poverty of species and aspect of underexploitation, the numbers of individual animals appear high, and in terms of the production of animal matter the islands may not differ significantly from continental areas.

Detailed quantitative studies are urgently needed in undisturbed oceanic islands of this kind, and the small number of interacting species may permit the assessment of the role of each one in the ecosystem.

Time was unfortunately not available for discussion of this paper.

The meeting's thanks were expressed to Professor D. Lewis for the hospitality of his Department, and to Dr and Mrs P. J. Newbould and their helpers for making the local arrangements.

THE ANNUAL GENERAL MEETING

The 41st Annual General Meeting began at 10 a.m. on Saturday, 9 January 1960. The following are the (unconfirmed) minutes of this meeting.

MINUTES OF 41ST ANNUAL GENERAL MEETING

The President, Professor N. A. Burges, took the chair in the Lecture Theatre of the Department of Botany, University College, London, at 10 a.m. on 9 January 1960.

(1) The minutes of the 40th Annual General Meeting, having appeared in *J. Ecol.*, **47**, 3, and being due to appear in *J. Anim. Ecol.*, **28**, 2, were taken as read, and approved.

(2) The following report of the Hon. Secretaries had been duplicated and circulated to members attending the meeting:

Report of the Honorary Secretaries for 1959

Meetings

During 1959 effect was given to the recommendations of the Programme Planning Committee constituted the previous year. Besides the Winter Meeting in Oxford devoted to a variety of ecological subjects, and the Summer Field Meeting in Galway, two specialized meetings were held in the spring—one on Freshwater Ecology at Reading and the other an intensive, four-day symposium on the Biology of Weeds at Oxford. In terms of attendance the response to these arrangements has been most encouraging: all were well attended, the numbers exceeding 100 at Oxford (January), 40 in Galway, 70 at Reading and 160 at Oxford (April).

The 40th Annual General Meeting of the Society was held during the Winter Meeting in the Department of Zoology and Comparative Anatomy, University of Oxford. The President, Professor N. A. Burges, took the chair at 10 a.m. on 3 January 1959. An account of the proceedings has appeared in *J. Ecol.*, **47**, 3, and will appear in *J. Anim. Ecol.*, **28**, 2.

Papers were read on Friday afternoon, 2 January, as follows: Miss K. Paviour-Smith—'The insect inhabitants of the birch-bracket fungus'; Professor W. T. Williams—

'Association analysis—an objective method for the analysis of vegetation by an electronic computer'; Dr J. M. Lambert—'The ecological implications of association analysis'; Mr P. Jewell—'The small vertebrate fauna of Salisbury Plain in Bronze Age times' and Dr D. Nichols—'Ecological problems concerning extinct sea-urchins'. An informal dinner was held in Jesus College, followed by a soirée in the Department of Zoology where a variety of interesting exhibits were on view, a feature of which was the extent to which they were illustrative of papers being delivered during the meeting.

Professor N. A. Burges delivered his Presidential Address on the morning of Saturday, 3 January. This, entitled 'Time and size as factors in ecology', will appear in both Journals. The remaining papers were: Dr R. D. Hughes—'The natural mortality of *Erioischia brassicae* (Diptera: Anthomyidae) during the egg stage'; Dr J. Warren Wilson —'Analysis of the spatial arrangement of foliage by two-dimensional and inclined point quadrats'; Mr R. Moreau—'The avifaunas of four archipelagos' and Dr L. W. Poel— 'Quantitative studies of soil aeration using an oxygen diffusion meter'. The Society's thanks are expressed to Professor Sir Alister Hardy for extending the hospitality of his Department, and to Professor G. C. Varley for attending to all local arrangements.

The meeting devoted to Freshwater Ecology took place in the Faculty of Letters, Reading, on 1 and 2 April, preceded by a soirée on 31 March.

1 April was devoted to a series of ten papers on freshwater subjects. Dr H. B. N. Hynes, Dr P. A. Horton, Dr K. H. Mann, Dr T. B. Reynoldson, Mr N. C. Morgan and Mr D. T. Crisp dealt with studies on freshwater invertebrates in Britain. Significant in comparison to papers read at a similar meeting in 1952 was the change in emphasis from purely field observation on the distribution of different species towards a more detailed and realistically quantitative approach dealing with one or a few species and involving laboratory and field experimentation as well as observation. Dr Rzóska discussed the zooplankton of the Nile and Dr Talling, Dr Prowse and Mr Edwards dealt with phytoplankton and freshwater vegetation. An audience of nearly eighty contributed a lively discussion to nearly every paper. On 2 April about twenty members were taken on an enjoyable and interesting excursion to freshwater habitats near Reading, notably the University's Laboratory on the River Thames and the headwaters of the River Pang. We are grateful to Dr Mann and his colleagues at Reading for the arrangements for a most successful meeting which left no doubt of the contemporary vigour of freshwater ecology.

The first of the projected series of British Ecological Society Symposia, devoted to the Biology of Weeds, was held in Oxford between 2 and 4 April, and was organized by Dr J. L. Harper who is to be congratulated on its success. Twenty-four papers were read by Members of the Society and invited speakers (including guests from overseas); these were grouped into an Introductory section, and sessions on Problems in the Taxonomy and Evolution of Weeds; The Dormancy and Dispersal of Weed Seeds; Population Studies, Interference and Competition; Special Weed Problems; Autecological Studies on Weed Species. An informal evening discussion proved to be of outstanding interest, lasting well into the following day. A volume containing the proceedings of the symposium has been prepared for publication under the editorship of Dr Harper, and is expected to be ready in April 1960. Grateful acknowledgment is made to a number of commercial concerns which responded to an appeal for contributions to a Publications Fund to provide financial backing for this volume.

The Summer Meeting, based on Galway, included excursions to saltmarshes south of Oranmore and a raised bog at Woodford; coastal, blanket bog and hill communities in Connemara; Loughs Carra and Mask; and the Burren district (two days). The whole meeting proved to be of exceptional interest and fine weather contributed to the enjoyment of the excursions. The Society is most grateful to Professor D. A. Webb who planned the meeting, gave an introductory talk on the region and led an evening discussion on the history and ecology of the Burren, to Mr W. A. Watts who supervised the organization, and to all others who helped to make it so successful.

Journals

Despite a dispute in the printing industry, the 1959 Volume of the *Journal of Ecology* was completed within the year. The first number contained 248 pages, with eight original

papers and three parts of the Biological Flora; No. 2 had 280 pages, thirteen papers, one Biological Flora account, ten book reviews; and No. 3 with 190 pages brought the total size of the volume to 719 pages and included ten papers, one contribution to the Biological Flora, two book reviews and an account of the Winter Meeting of the Society held in January 1959. The parts of the Biological Flora appearing in this volume were *Quercus* L. (*Q. robur* L. and *Q. petraea* (Matt.) Liebl., *Q. borealis* Mich. var. *maxima* Sarg., *Q. cerris* L. and *Q. ilex* L.) by E. W. Jones; *Dactylis glomerata* L. by A. R. Beddows; *Hornungia petraea* (L.) Rchb. by Denis Ratcliffe; *Cynosurus cristatus* L. by R. W. Lodge; and *Agrostis setacea* Curt. by R. B. Ivimey-Cook. The Council, Publications Committee and Hon. Treasurer negotiated a favourable agreement with the American publisher Mr W. Johnson, whereby he will reprint the out-of-print back volumes of the *Journal of Ecology*, and make them available again for sale. The Society will receive a commission from these sales, and there is good reason to believe that our association with Mr Johnson will help to increase sales of both current and back numbers in the future. In the past year current sales have been satisfactorily maintained and sales of back numbers have shown an encouraging increase. Pressure on space in the *Journal of Ecology* is still a major problem and the Editors have had to continue to insist on contributors being rigorously brief. The Society, however, received a grant of £1000 from the Royal Society which cased the immediate financial burden of the Journal. We are also pleased to report that the Editors have been able to arrange with Mrs Moullin (who prepared the Index for Volumes 1-20) for her to start immediately on the preparation of a new Index for Volumes 21 onwards.

The first part of Volume 28 of the *Journal of Animal Ecology* had 188 pages and consisted of ten original papers, reviews and abstracts. Publication of the second part has been delayed by the printers' strike until the new year, but when published the part will bring the volume up to the normal size for the past few years. Sales of both current and back numbers of the Journal continue at a very satisfactory level.

Membership

During the year twenty-six members were lost to the Society through resignation and four by death. The total membership at the end of 1959 stands at 1057; the increase in subscriptions in 1958 probably lost the Society about 8% of its members, but new members have continued to join at the satisfactory rate of about eighty in the year.

The *Council* met three times during the year to conduct its usual business. It has continued to be advised by its two Committees. The Standing Committee on Publications has met four times and dealt with the detailed problems of the publication and finances of the Journals. The Programme Planning Committee has met twice and outlined a plan for an annual symposium for the next 3 years, as well as the regular annual winter and summer excursion meetings. The Council hopes to keep in touch with moves to create an international organization for ecology, and to use the Society's influence to direct these moves along useful lines.

In conclusion we are able to report that the Society continues to grow in size and the year's meetings have been well attended and stimulating in content. The arrangements with Mr Johnson which will eventually lead to complete sets of the *Journal of Ecology* again being available, and the first of a new series of annual symposia have been the highlights of the Society's year. We feel, however, there is still no room for complacency while there are more and more societies and meetings competing for our members' interest and while, for example, the young New Zealand Ecological Society can have attendances of a hundred at its meetings in a country with but 4% of the population of Britain.

Finally, we would like again to thank all those who have given the Society assistance and hospitality at its meetings during the year, and also to thank our fellow Officers and Councillors for their continued support and assistance and express our gratitude to those who have given us secretarial help.

C. H. Gimingham
E. D. Le Cren
Honorary Secretaries

December 1959

Dr C. H. Gimingham commented briefly on this report which was adopted.

(3) Dr F. H. Whitehead presented the provisional report of the Hon. Treasurers. Following the developments of recent years, including the sale of back numbers of the *Journal of Ecology* to Mr Johnson and a grant from the Royal Society, the Society's finances have returned to a reasonably healthy position. With these aids it is expected that the 1959 accounts will show a deficit of only about £200 as compared with £1414 in 1958; it is hoped that increases in the price of back numbers of the Journals will during the coming year enable the Journals' accounts to show a slight profit instead of a loss.

(4) In discussing the Society's financial position and its bearing on the prices of Journals and rates of subscriptions, the Treasurer pointed out that it had already been agreed to raise the price of the *Journal of Ecology* to non-members while it was proposed that a proportionate increase in the price of the *Journal of Animal Ecology* should take effect from 1961. It seemed that, at least for the present, no increase in membership subscriptions was necessary. A discount of 25% to members purchasing back numbers of the Journals, provided these are ordered through the Secretaries, had been proposed.

It was proposed from the chair and agreed that the Treasurer's recommendations should be accepted.

(5) Professor P. W. Richards, presenting his report as editor of the *Journal of Ecology*, said that his main problem was the difficulty of compressing a large volume of good-quality contributions into a limited space. Referring to the fact that the Journal is international, carrying important contributions covering the whole field of ecology as well as purely British work, he stressed the desirability of maintaining a suitable balance. Priority in date of appearance was being given to short papers (especially those reporting experimental work).

Mr H. C. Gilson, Editor of the *Journal of Animal Ecology*, expressed his regret over the delay in the appearance of part 2 of Volume 28 owing to the printers' strike. He hoped that with a slight increase in size the normal period between acceptance of a manuscript and its appearance in the Journal would not exceed 6-7 months. In answer to questions he said that occasionally papers concerned with the descriptive ecology of areas outside the British Isles were rejected; some had appeared later in other journals.

(6) Dr D. E. Coombe reported on behalf of the editors of the Biological Flora and referred to the accounts which had appeared in the past year, mentioning the extra allowance of pages for the account of *Quercus* spp. in view of their exceptional ecological importance. He welcomed the submission of accounts in the stage of first draft, to permit consultation between author and editors before preparation of the final version.

(7) On the proposal of the retiring President, the meeting unanimously elected Professor J. B. Cragg as President.

On assuming the chair, Professor Cragg expressed the Society's thanks to Professor N. A. Burges for his active interest in the Society's affairs during his period of office.

The following, having been nominated by Council, were proposed from the chair and unanimously elected as Officers and Members of Council:

Vice-President: P. W. Richards
Hon. Secretaries: C. H. Gimingham, E. D. Le Cren
Hon. Editors (*Journal of Ecology*): P. W. Richards, D. E. Coombe
(*Journal of Animal Ecology*): H. C. Gilson
Members of Council (to retire in 1964): A. R. Clapham, W. H. Dowdeswell, E. A. G. Duffey, P. J. Newbould

After a short adjournment, Professor Cragg nominated the following for election as Honorary Members of the Society: Capt. C. Diver, Mr C. Elton, and Dr A. S. Watt. This was agreed with acclamation.

C. H. Gimingham

SPRING SYMPOSIUM, 1960

The second symposium organized by the Society was held at Durham from 28 to 31 March 1960 on 'The Exploitation of Natural Animal Populations'. About 130 people attended, including visitors from Canada, Denmark, Holland, Italy, Portugal, Sweden, U.S.A. and U.S.S.R. Most of us lived in St Mary's College or Grey College and did a great deal of our talking during and after meals, one of the great advantages of meetings organized in this way. We also had two crowded and uninhibited evenings' discussion in St Mary's, on topics which at least started out on the subjects of (*a*) 'Is it relevant to construct a comparative population dynamics?' and (*b*) 'The response of populations to exploitation, and the operation of density-related factors'. On the first evening we saw some films about whaling and other forms of exploitation, and on the last we were kindly given a reception by the Council of the Durham Colleges. Sir James Duff received us in the Castle, and we had dinner in the magnificent banqueting hall.

The papers were concerned with a wide variety of animals from whales to *Daphnia*, and will be published fairly soon. It is sometimes hard to know what one gets out of a varied assortment such as this; but despite the diversity of the species, techniques, and nature of the data, there were common features about the problems. It seemed to be fairly generally agreed that the speakers had had something stimulating to contribute, and there was a fair amount of discussion.

The delivery of the papers was less good. In spite of instructions about keeping their diagrams simple, many people's slides were poorly labelled and overcrowded with detail. Some speakers had obviously not rehearsed their talk, gave too many details at the start, and crammed their main points into the last few minutes, or left some of them out, or ran over their time. Far too few realized that it might be difficult for a continental visitor to understand English spoken to the blackboard or screen, mumbled, or delivered at high speed. These errors were not more evident than they usually are at scientific meetings, and a number of excellent speakers made up for the rest; it is nevertheless astonishing how much mutual suffering is inflicted through lack of attention to form.

The great success of this symposium was firstly due to Mr E. D. Le Cren. He not only managed to attract a great deal of talent, but succeeded in getting advance abstracts out of the speakers (a great achievement and most useful), and arranged a rather crowded timetable in a pleasing sequence that was not too exhausting. Secondly, Dr M. W. Holdgate made all arrangements for our comfort (we were warm and well fed), and everything seemed to work without a hitch. Finally, Professor J. B. Cragg, as President and host, provided the all-important factor of the right atmosphere, in spite of being in the early stages of an illness that laid him low on the last afternoon.

DENNIS CHITTY

THE BRITISH ECOLOGICAL SOCIETY

Officers and Council for the Year 1960

President: J. B. CRAGG — *Vice Presidents*: D. CHITTY, P. W. RICHARDS

Honorary Treasurers:

F. H. WHITEHEAD — Imperial College Field Station, Selwood Park, Sunninghill, Berks.

J. L. HARPER (receives subscriptions) — Department of Agricultural Botany, University College of N. Wales, Bangor, Caerns.

Honorary Secretaries:

C. H. GIMINGHAM (membership) — Department of Botany, University of Aberdeen, Old Aberdeen.

E. D. LE CREN (Council) — The Ferry House, Far Sawrey, Ambleside, Westmorland.

Honorary Editors of the Journal of Ecology: P. W. RICHARDS and D. E. COOMBE

Honorary Editor of the Journal of Animal Ecology: H. C. GILSON

Council (together with Officers as above):

Retiring: 1961	1962	1963	1964
D. J. CRISP	M. ASHBY	F. FRASER DARLING	A. R. CLAPHAM
M. W. HOLDGATE	F. J. BINGLEY	J. L. HARLEY	W. H. DOWDESWELL
C. D. PIGOTT	P. GREIG-SMITH	K. H. MANN	E. A. G. DUFFEY
H. V. THOMPSON	L. A. HARVEY	J. WARREN-WILSON	P. J. NEWBOLD

Honorary Editors of the Biological Flora:
A. R. CLAPHAM, D. E. COOMBE, C. D. PIGOTT, P. W. RICHARDS

The British Ecological Society was founded in April 1913, when it replaced the British Vegetation Committee (founded in 1904). The object of the Society is to promote and foster the study of Ecology in its widest sense. This it does by publishing the *Journal of Ecology* and the *Journal of Animal Ecology*, and by holding regular meetings when papers are read and symposia and discussions on subjects of current ecological interest are held. At present these meetings are held in early January, March or April, and July, in London, Oxford or Cambridge or a provincial centre; the July meeting is devoted primarily to excursions to places of ecological interest.

MEMBERSHIP of the Society is open to all, whether or not they reside in the British Isles, who are genuinely and personally interested in Ecology and wish to receive the Society's journals for their own use. The minimum subscription for membership is 40*s*., due on 1 January each year. This entitles members to receive *one* of the two journals, to attend the meetings and make use of other facilities that the Society may offer, to vote in the election of Council and Officers and be eligible for election to Council and Office. For a subscription of 70*s*. members may receive *both* journals.

ASSOCIATE MEMBERSHIP of the Society is open to those who wish only to attend meetings. Associates pay an annual subscription of 7*s*. 6*d*. and do not have the right to receive a journal or vote at a meeting of the Society.

Local Natural History Societies, Field Clubs and other similar bodies are eligible for a special membership of the Society.

Full details of membership and an application form may be obtained on request from either of the Honorary Secretaries.

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WORLD-LIST ABBREVIATION: *J. Anim. Ecol.*

CONTENTS

PAGE

J. M. Colebrook. Plankton and water movements in Windermere . . . 217

J. M. Colebrook. Some observations of zooplankton swarms in Windermere . 241

E. White. The distribution and subsequent disappearance of sheep dung on Pennine moorland 243

J. C. Coulson. A study of the mortality of the starling based on ringing recoveries 251

Peter S. B. Digby. Midnight-sun illumination above and below the sea surface in the Sörgat, N.W. Spitsbergen, and its significance to plankton . . 273

J. Phillipson. The food consumption of different instars of *Mitopus morio* (F.) (Phalangida) under natural conditions 299

W. J. Stower, D. E. Davies and I. B. Jones. Morphometric studies of the desert locust, *Schistocerca gregaria* (Forsk.) 309

D. C. Drummond. The food of *Rattus norvegicus* Berk. in an area of sea wall, saltmarsh and mudflat 341

S. Markowski. Observations on the response of some benthonic organisms to power station cooling water 349

R. D. Hughes and B. Mitchell. The natural mortality of *Erioischia brassicae* (Bouché) (Dipt., Anthomyiidae): life tables and their interpretation . . 359

C. L. Batcheler. A study of the relations between roe, red and fallow deer, with special reference to Drummond Hill Forest, Scotland 375

J. B. Free. The behaviour of honeybees visiting flowers of fruit trees . . 385

R. A. Davis and A. G. Jenson. A note on the distribution of the coypu (*Myocastor coypus*) in Great Britain 397

G. C. Varley and G. R. Gradwell. Key factors in population studies . . 399

Reviews 403

Books received 409

Abstracts 411

British Ecological Society

Accounts for 1959 429

Spring Meeting, 1959 432

Symposium—The Biology of Weeds, Spring 1959 434

Summer Meeting, 1959 435

Winter and Annual General Meeting, 1960 439

Symposium—The Exploitation of Natural Animal Populations, Spring 1960 448

Notice to Contributors . . . . . Cover ii

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